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Number 1, 1990

Fishery Bulletin

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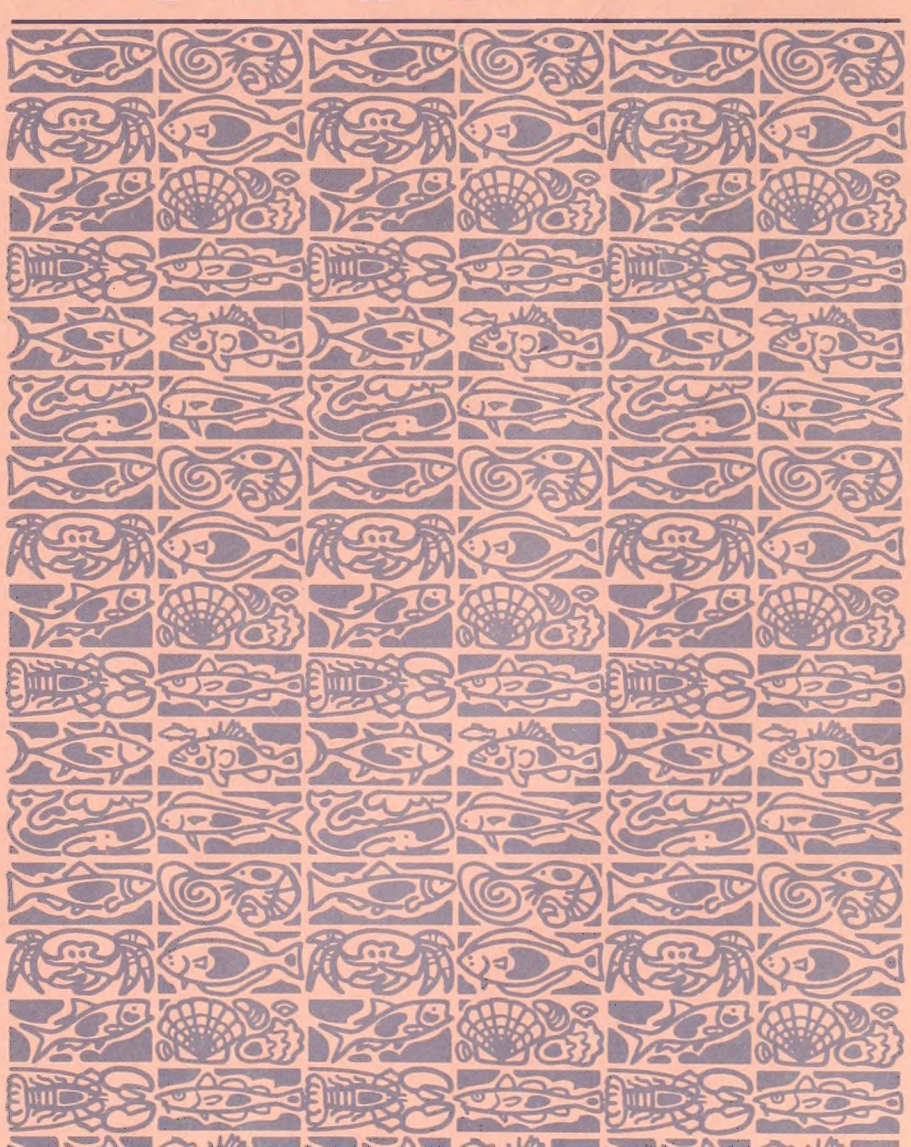

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Abstract.–The summer flounder *Paralichthys dentatus* spawned throughout the Mid-Atlantic Bight and Georges Bank during 1977–85. Spawning peaked in fall but extended from September through January. Planktonic larvae (2–13 mm) were most abundant in the Mid-Atlantic Bight September–May. At approximately 11–14 mm, some larvae entered New Jersey estuaries; but their occurrence, especially during winter and early spring, was sporadic. Young-of-the-year were more frequently collected after May. During the first summer inshore they grew rapidly and reached 160–320 mm TL. Young-of-the-year emigrated from the estuaries in fall and were most abundant on the shallow portions of the adjacent continental shelf. Some evidence suggests that young-of-the-year in the northern Mid-Atlantic Bight reach a larger size than those from the southern portion. An hypothesis to explain the observed rarity of small juveniles in northern estuaries in some years is that some juveniles utilize the continental shelf as a nursery and enter estuaries at a larger size. This hypothesis requires testing.

Patterns of Summer Flounder *Paralichthys dentatus* Early Life History in the Mid-Atlantic Bight and New Jersey Estuaries

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Fishery Bulletin, U.S. 88:1–12.

The summer flounder *Paralichthys dentatus* inhabits estuarine and continental shelf waters from Nova Scotia (Leim and Scott 1966) to Florida (Gutherz 1967). Over much of this range it supports important commercial and recreational fisheries (Grosslein and Azarovitz 1982). The economic importance of *P. dentatus* has prompted research on various aspects of its biology (see Scarlett 1982, Grosslein and Azarovitz 1982, Rogers and Van Den Avyle 1983), but the spatial and temporal patterns of spawning and the nursery areas are not well known. Our understanding of the timing and distribution of spawning in the Mid-Atlantic Bight is based on examination of adult gonads (Morse 1981) and larval surveys (Smith 1973, Smith et al. 1975, Morse et al. 1987). Spawning occurs at temperatures of 12–19°C (Smith 1973), eggs and larvae are pelagic, hatching in the laboratory occurs approximately 48–96 hours after fertilization at 15–21°C (Johns and Howell 1980, Johns et al. 1981), and the pelagic larvae begin transformation at 9–12 mm SL (Smith and Fahay 1970, Smigielski 1975).

Major nursery areas are assumed to occur in estuaries from Virginia and south (Poole 1966, Powell and Schwartz 1977, Grosslein and Azarovitz 1982), although juveniles also occur in estuaries in the northern Mid-Atlantic Bight (Poole 1961, Pearcy and Richards 1962, Pacheco and Grant 1973). Juveniles, presumably, leave estuaries in fall, migrate offshore to overwinter, and return to the estuaries in spring with the adults (Hamer and Lux 1962, Murawski 1970). Although some individuals have been found north and east of their estuarine and offshore tagging locations,

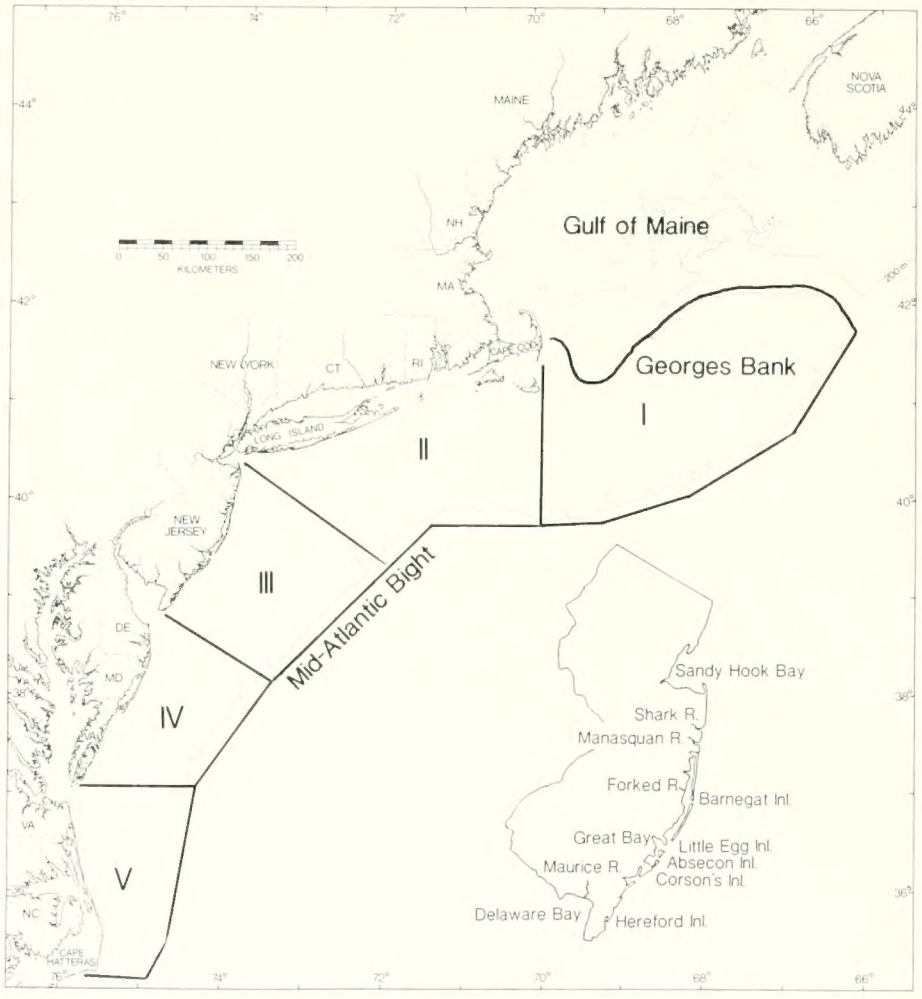

Figure 1
Study area with subarea boundaries and important localities mentioned in the text.

others returned to the original tagging locations in estuaries.

Conflicting evidence concerning the distribution of different stocks or subpopulations hampers interpretation of the patterns of reproduction and identification of nursery areas. Several authors have suggested that Mid-Atlantic Bight and North Carolina populations may be separate (Ginsburg 1952, Smith and Daiber 1977, Wilk et al. 1980). An alternate interpretation is that inshore populations from Virginia to North Carolina may form a separate population from those to the north and offshore (Delaney 1986).

Herein we attempt to clarify the patterns of reproduction and early life history of *P. dentatus* in the Mid-Atlantic Bight. Our interpretations are based on extensive collections of eggs, larvae, and first-year juveniles from continental shelf and estuarine waters.

Materials and methods

Data for eggs, larvae and first year juveniles of *P. dentatus* collected over the Mid-Atlantic Bight continental shelf and in New Jersey estuaries (Fig. 1) derive from sources given in Table 1 and from Marine Resources Monitoring, Assessment and Prediction (MARMAP) surveys (Sherman 1980, 1986) by the National Marine Fisheries Service (NMFS). These surveys were conducted at monthly to bimonthly intervals over the continental shelf from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia. Sampling methodology can be found in Sibunka and Silverman (1984) and Morse et al. (1987). Collections made with 61-cm bongo frames fitted with 0.505-mm mesh nets were corrected for the depth of tow and volume of water filtered and expressed as number per unit volume of sea surface. For graphic display of the egg and larval distribution and abundance, the catches per

Table 1

Summary and sources of *Paralichthys dentatus* data and specimens of young-of-the-year from New Jersey, reexamined for this study.

Study area	Collection method	Collection period	Number of individuals	Length range (mm TL)	Source
Southern New Jersey estuaries and Delaware Bay	Miscellaneous trawls, seines	1930s–1972	538	10–320	Allen et al. 1978 de Sylva et al. 1961 Milstein and Thomas 1976 Acad. Nat. Sci. Phila. collections
New Jersey inlets	1-m plankton net (0.5 mm mesh), trawls	1962–72	380	5–21	Festa 1974
Maurice River and vicinity of Atlantic City	1-m plankton net (0.5 mm mesh)	1975–77	6	15–19	Himchak 1982
Barnegat Bay	Power plant screens, trawls	1976–80	1091	10–330	Vouglitois 1983 Tatham et al. 1977
Great Bay	Recreational fishery creel survey	1967–76	1905	230–300	Festa 1979
New Jersey offshore	Otter trawl	1985	173	16–300	Halgren and Scarlett 1985
Manasquan River	Trawl	1984–86	128	35–320	Scarlett 1989

10 m^2 within each 25-km^2 block in the survey area were averaged for all years combined. Additional *P. dentatus* collections were made with a 0.5-m net (1.8 mm mesh) during 1987 from Little Sheepshead Creek which is immediately adjacent to Little Egg Inlet, New Jersey (Fig. 1). Lengths of larvae (Table 4) were recorded as millimeters (mm) notochord length (NL) or standard length (SL). Lengths for transforming individuals and larger young-of-the-year (YOY) (Figs. 4,5) are presented as total length (TL). For purposes of comparison, SL = 0.650 + 0.778 TL.

Our assignment of *P. dentatus* specimens to the YOY group from inshore and offshore data sets was based on size frequencies and ages derived from scales. Ageing criteria were based, in part, on the protocol developed by Smith et al. (1981). Data for YOY collected over the continental shelf were taken during fall bottom-trawl surveys conducted by the Northeast Fisheries Center, NOAA. Sampling methodology for these surveys is described by Azarovitz (1981).

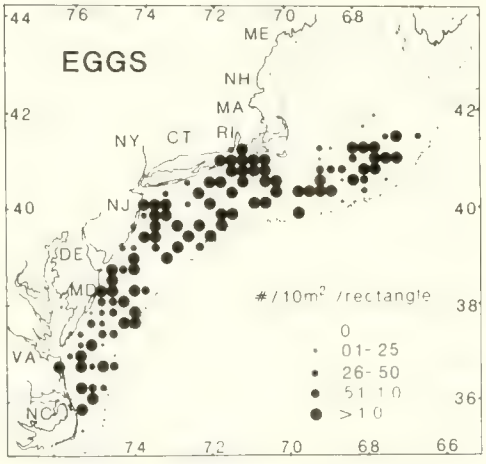

Figure 2

Distribution and abundance (cumulative mean no./10 m^2 of sea surface) of *Paralichthys dentatus* eggs from MARMAP collections during 1979–81, 1984, and 1985.

Results

Offshore egg distribution

Composite collections of *Paralichthys dentatus* eggs during 1979–85 indicate that spawning occurs from Georges Bank to Cape Hatteras from nearshore to the edge of the continental shelf (Fig. 2). Eggs were most abundant in samples from subareas II–V (Fig. 1, Table 2). Eggs were collected as early as September (except in subarea I) and as late as December and January in subareas I, II, and IV, although the number of stations sampled was small (subarea III) or zero (subareas IV and V) in December (Table 2). In all subareas the highest frequency of occurrence and greatest abundance occurred in October and November (Table 2).

Offshore larvae distribution

The spatial distribution of larvae was similar to that of the eggs except that larvae were much less numerous in subarea I (Fig. 3, Table 3). In general, larvae were most abundant in subareas II, III, and V (Table 3).

Table 2

Abundance of *Paralichthys dentatus* eggs (mean no. 100 m⁻² of sea surface) from MARMAP surveys during 1979–81, 1984, and 1985, by subarea and month. occ = number of stations where eggs occurred; nst = number of stations sampled; dash indicates no eggs collected; ns indicates no samples.

Subarea	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
I Georges Bank												
	–	–	–	45.2	42.8	2.0	0.9	–	–	–	–	–
(occ)	0	0	0	42	17	1	1	0	0	0	0	0
(nst)	149	176	79	345	143	97	109	80	191	252	121	75
II Southern New England												
	–	–	1.3	171.8	97.1	19.8	–	–	–	–	–	–
(occ)	0	0	1	46	27	3	0	0	0	0	0	0
(nst)	152	116	35	143	63	58	74	13	183	109	49	57
III New Jersey												
	–	–	2.8	4.4	133.7		–	–	–	–		–
(occ)	0	0	2	25	15	0	0	0	0	0	0	0
(nst)	102	64	39	83	54	5	38	57	118	76	40	61
IV Delmarva Peninsula												
	–	–	14.3	86.3	83.2	ns	1.2	–	–	–	–	–
(occ)	0	0	12	10	21		1	0	0	0	0	0
(nst)	97	62	79	34	64		42	84	110	71	43	67
V Virginia Capes to Cape Hatteras												
	–	–	1.6	48.2	121.0	ns	–	–	–	–	–	–
(occ)	0	0	2	5	17		0	0	0	0	0	0
(nst)	64	71	58	25	48		34	66	83	137	162	74

Table 3

Abundance of *Paralichthys dentatus* larvae (mean no./100 m⁻² of sea surface) from MARMAP surveys during 1977–85, by subarea and month. occ = number of stations where larvae occurred; nst = number of stations sampled; dash indicates no larvae collected; ns indicates no samples.

Subarea	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
I Georges Bank												
	–	–	–	7.0	15.6	5.9	1.8	1.8	–		–	
(occ)	0	0	0	20	12	7	2	2	0	0	0	0
(nst)	162	184	31	371	164	137	106	118	200	241	225	109
II Southern New England												
	–	–	5.9	75.5	177.7	112.6	4.7	11.4	0.2			
(occ)	0	0	3	73	26	54	3	6	1	0	0	0
(nst)	169	170	29	186	49	113	49	56	207	184	154	124
III New Jersey												
	–		0.3	13.4	141.7	47.9		5.9	0.6		–	–
(occ)	0	0	1	26	23	10	0	5	2	0	0	0
(nst)	141	122	14	116	64	30	79	119	160	144	135	128
IV Delmarva Peninsula												
	–	–	–	53.8	52.9	27.3		2.3	0.1	0.7	0.2	
(occ)	0	0	0	13	23	6	0	7	1	2	1	0
(nst)	91	113	83	46	65	17	79	130	154	93	129	103
V Virginia Capes to Cape Hatteras												
				3.7	176.8	ns		1.3	3.6	17.7	3.4	–
(occ)	0	0	0	4	30		0	3	8	14	8	0
(nst)	65	80	72	34	48		79	113	103	56	97	73

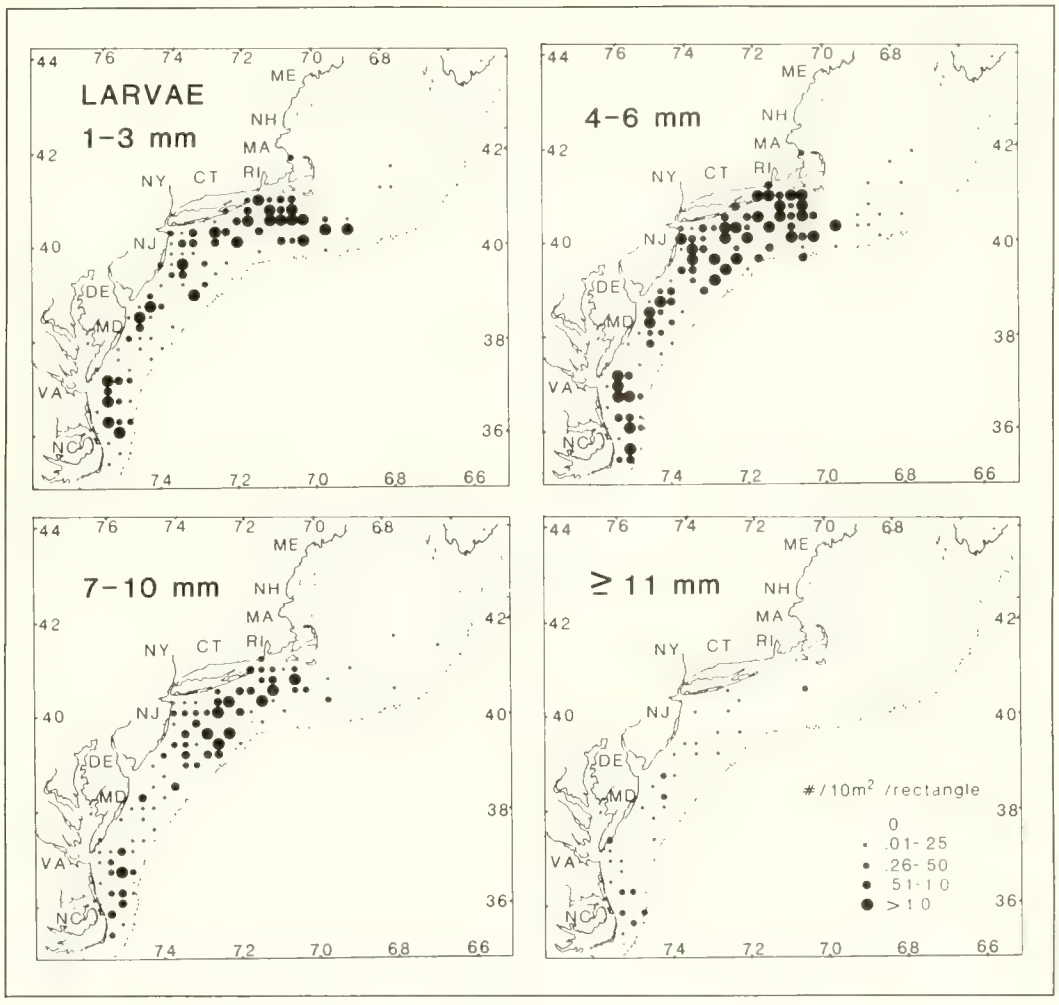

Figure 3

Distribution and abundance (cumulative mean no./10m^2 of sea surface) of *Paralichthys dentatus* larvae by length during 1977–84.

Small larvae (<6 mm) were clumped in three regions (Fig. 3): Subarea II to northern subarea III, northern subarea IV, and subarea V. The northern and southernmost of these groupings are also apparent for larvae of 7–10 mm, but there is no well defined pattern for larger larvae.

Larvae were collected September–May, depending on location, but in most subareas the peak abundance occurred in November (Table 3). Larvae were captured as early as September in subareas II and III. The latest captures were during May in subareas IV and V. Larvae occurred over 5–7 months within the study area (Table 3). The shortest duration of occurrence was in subarea I (October–February), and the longest was in subareas IV and V (October–May). For most subareas, larval catches were low or zero in January followed by a slight increase in February. The most southerly subarea (V) showed a smaller peak in April. Individual years (see Morse et al. 1987) revealed similar patterns in timing and location of eggs and larvae as found in the composite data (Table 3).

As expected from the timing of peak egg abundance, the smallest larvae (<6 mm) were most abundant October–December (Table 4). Small larvae (4–8 mm) occurred in April, although we collected no eggs February–April which could have accounted for these larvae. The largest larvae (≥11 mm) were abundant November–May with peaks in November–December and March–May.

Inshore occurrence of larvae and juveniles

Transforming *P. dentatus* have been collected from most of the major inlets adjacent to subarea III along the New Jersey coast. Reexamination of data collected in New Jersey estuaries (Table 1) and our own collecting efforts indicate transforming larvae have occurred

Table 4

Abundance (mean no./100 m² of sea surface) of *Paralichthys dentatus* larvae from MARMAP surveys during 1977–85, by month and length.

Length (mm SL)	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
2		73.6	53.0	7.2					
3	9.5	1048.0	815.6	141.1					
4		563.1	853.0	291.7		2.2		6.5	
5		238.1	509.7	308.6	4.5	12.1		12.5	6.5
6	4.6	106.8	461.5	213.9	8.9	13.7		4.6	
7		75.7	318.2	194.6	4.5	29.0		28.9	
8	4.6	46.8	117.8	166.0	10.0	94.1	8.9	4.5	8.8
9		1.9	11.8	80.6	4.5	23.0	5.0	12.6	
10			22.1	56.5	5.6	30.6	15.7	4.0	
11		1.9	3.5	12.9	4.4	3.8	14.0	16.9	12.1
12						3.5	9.1	3.4	5.4
13			5.3	3.1			1.7	11.8	2.0
>13				14.7					1.5

in Sandy Hook Bay, Shark River Inlet, Manasquan Inlet, Barnegat Bay, Little Egg Inlet, Absecon Inlet, Corson's Inlet, and the Maurice River (Fig. 1). These larvae were in the range 8–21 mm ($n = 378$), but most were 11–14 mm. In Manasquan Inlet larval abundance was quite high, with counts per half-hour set reaching 31 larvae on 24 October 1967, 44 on 28 November 1963, 34 on 2 December 1966, and 64 on 5 December 1963 (Festa 1974).

Movement of transforming individuals through inlets in New Jersey occurs primarily October–December (Fig. 4). However, a few larvae have been collected as late as February (15–17 mm TL, $n = 2$) in Little Sheepshead Creek inside Little Egg Inlet (this study); in March and May (15.0–19.0 mm TL, $n = 4$) in the Maurice River off Delaware Bay; in March in Manasquan Inlet ($n = 1$) and Corson Inlet ($n = 1$); and February, March, and April in Absecon Inlet (10.6–13.8 mm TL, $n = 7$) (Table 1). The extensive collections in the Manasquan and Shark River inlets (Festa 1974) produced relatively large numbers that are depicted as the first peak of 10–20 mm individuals in October in Figure 4. Other collections suggest that some of these individuals may attain a size of 30–50 mm by December, but these occurrences have been sporadic. During 1975–80, *P. dentatus* of 30–50 mm only occurred in winter 1975. The available data are sparse for YOY January–April (Fig. 4). This same cohort was represented by a few individuals in May (30–50 mm and perhaps up to 90 mm), more individuals in June (30–140 mm) and accounts for the dominant peak July–October when they reach a size of 160–320 mm. As a result, in October there were two well-defined length-frequency modes: a mode around 10 mm that represents transforming individuals, and a larger mode (160–320 mm) that represents individuals 1 year older. In a subsample ($n = 111$) of *P. dentatus* collected during the period September– November (larger mode in Figure 4), 97% of the scales lacked an annulus; thus, by convention (Smith et al. 1981), they are considered to be YOY, although they are 1 year older than the transforming specimens (smaller mode in Figure 4).

Fall distribution of YOY

Young-of-the-year (160–320 mm) apparently move out of estuaries in fall with adults. By November, YOY are less abundant inshore (Fig. 4) but are well represented in NMFS continental shelf trawl surveys (Fig. 5). This same size class appeared as a definite peak (~200–270 mm) in September 1985 trawl collections off the coast of New Jersey (Halgren and Scarlett 1985). YOY individuals are distributed inshore from Long Island to south of Cape Hatteras at this time of the year (Fig. 6) with larger individuals apparently more abundant north of Delaware Bay (Fig. 7).

Discussion

Timing and location of spawning and development

The geographical patterns of reproduction observed during 1979–85, as measured by the distribution and abundance of eggs (Fig. 2), were similar to those reported for 1965–66 (Smith 1973). An exception is the report (possibly a result of misidentifications) of spawning in July in Narragansett Bay (Herman 1963). Our sampling in 1980–86 extended farther north and east

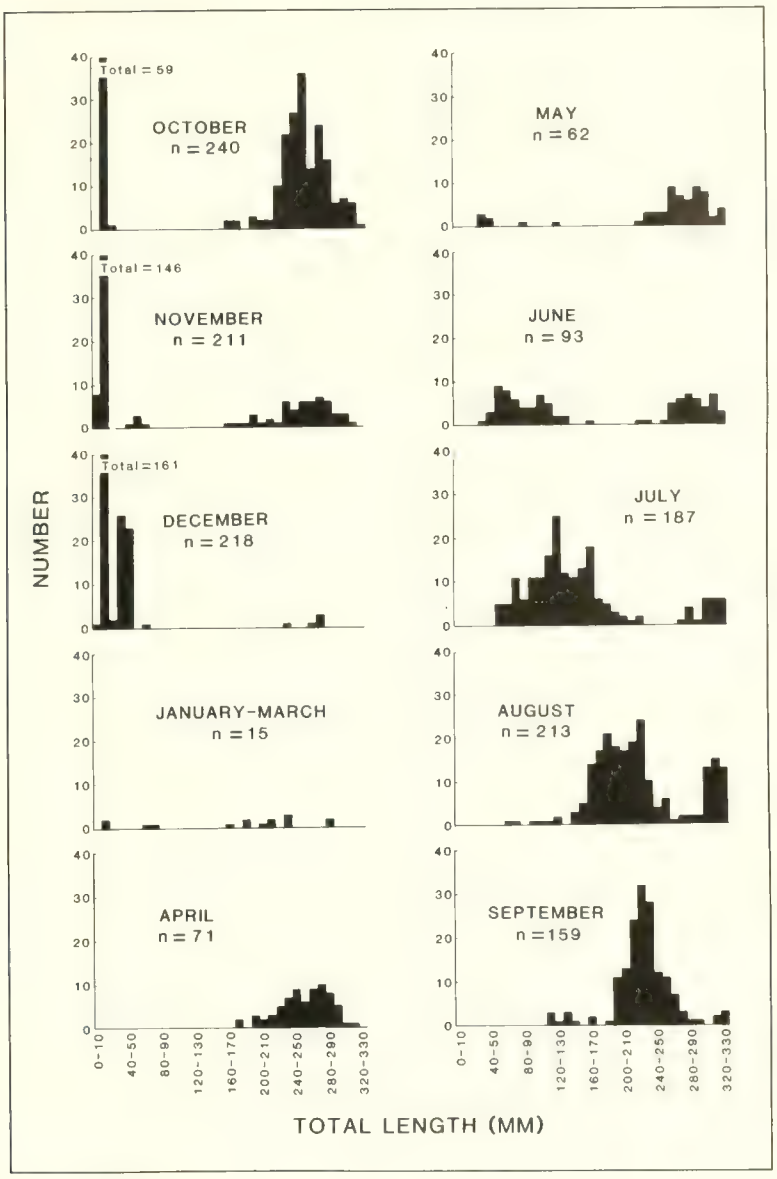

Figure 4
Cumulative monthly length frequencies of juvenile *Paralichthys dentatus* from northern New Jersey (Barnegat Bay and north) estuaries over several years. See Table 1 for data sources.

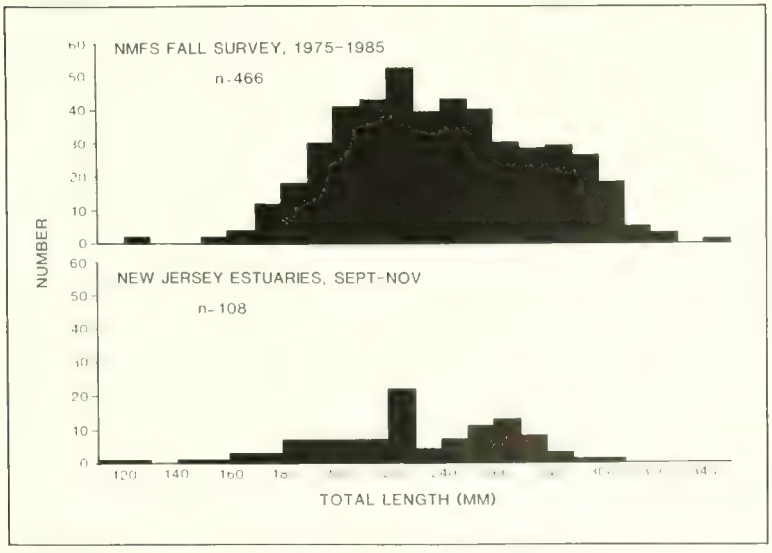

Figure 5
Length-frequency distribution of juvenile (0 age) *Paralichthys dentatus* from the Mid-Atlantic Bight continental shelf (NMFS September–November bottom-trawl surveys) and New Jersey estuaries.

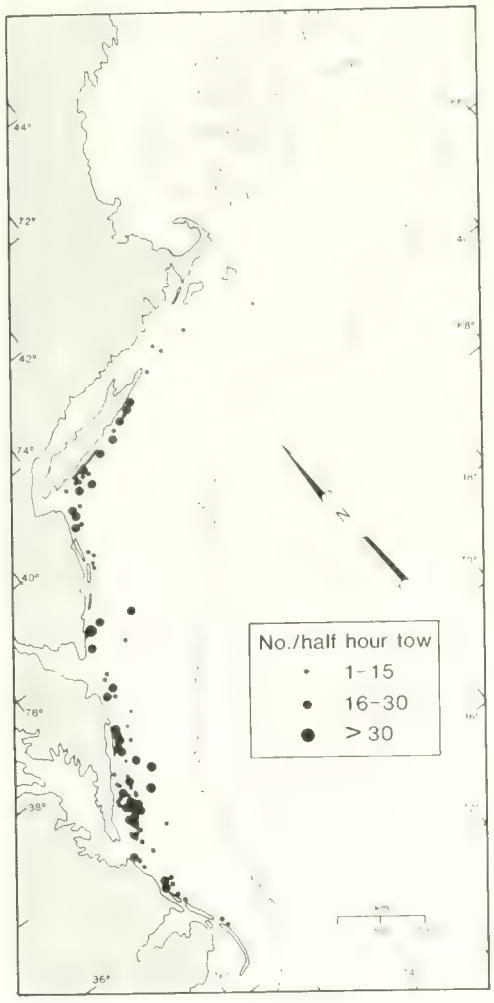

Figure 6

Geographical distribution of young-of-the-year (0 age) *Paralichthys dentatus* (NMFS September–November bottom-trawl surveys), 1982–86, expressed as number per half-hour tow.

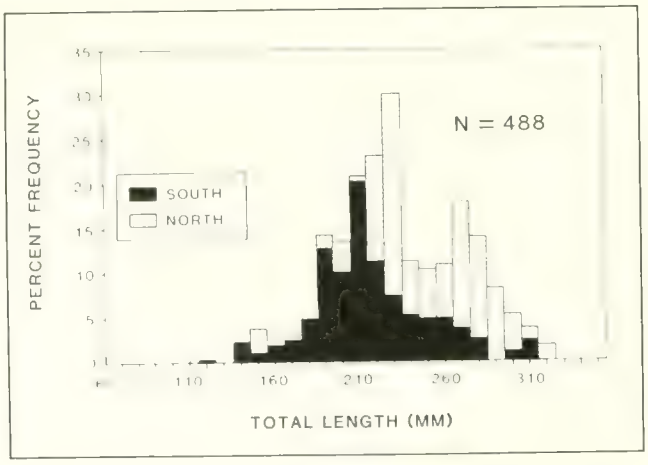

Figure 7

Length-frequency distribution of young-of-the-year *Paralichthys dentatus* in NMFS fall bottom-trawl surveys north and south of Delaware Bay.

than Smith's (1973), thus we can confirm that extensive spawning during this period occurred in subarea II, and extended to subarea I (Fig. 2, Table 2). In fact, subarea II (Fig. 1) provided the largest collections of eggs (Table 2) and larvae (Table 3). Although Smith (1973) reported the center of abundance to be off New Jersey and New York in 1965–1966, we found extensive reproduction during 1980–1986 occurred from New York to Massachusetts. Spawning was most pronounced in fall, with the earliest in the northern and the latest in the southern subareas (Table 2). The spawning period observed in this study is consistent with that of other studies (Hildebrand and Schroeder 1928, Smith 1973, Smith et al. 1975, Morse 1981) in the Mid-Atlantic Bight.

The above locations and timing of spawning, deduced from egg collections, were corroborated by collections of larvae. Small larvae were most abundant in early fall in subarea II but occurred into early spring in the southern subareas (Table 3).

Larvae of all sizes were found over the continental shelf throughout the study area (Fig. 3). Thus, there appeared to be no pronounced movements by larvae out of the major spawning areas as might be predicted from the general southerly or southwesterly flow reported for much of the Mid-Atlantic Bight (Bumpus and Lauzier 1965, Norcross and Stanley 1967). The only apparent exception is subarea I where egg collections (Fig. 2, Table 2) indicated spawning occurred, yet few larvae were collected (Fig. 3). Stronger currents in the prevailing flow off the southern and western portions of Georges Bank into the northern Mid-Atlantic Bight (Colton and Temple 1961, Butman and Beardsley 1987) might explain this exception.

Estuarine recruitment and growth

The movement of larval, transforming, and possibly juvenile *P. dentatus* into estuaries occurs over an extended time period. The collection of *P. dentatus* in New Jersey inlets October–April is consistent with the prolonged spawning period in the adjacent waters of subareas II and III (Table 3). Also, the peak in spawning in these areas in October and November may be reflected in the relatively abundant catches of small individuals (<20 mm TL) in October–December (Fig. 4).

Most authors have assumed that transforming *P. dentatus* move into estuarine nursery areas (see Rogers and Van Den Avyle 1983 for review). From

the available evidence, we conclude that at least a portion of the *P. dentatus* do this in New Jersey estuaries. It is clear that at sizes larger than approximately 11 mm SL, they become scarce in continental shelf plankton collections (Fig. 3) and that they can be collected in New Jersey inlets, usually at sizes of 11–14 mm TL. In addition, the larger juveniles have been collected, at least from power plant screens, with some regularity (Fig. 4). In some years larger YOY (240–300 mm) are clearly represented in recreational catches in New Jersey estuaries (Festa 1979). Despite this pattern, it is not always easy to collect small juvenile *P. dentatus* in New Jersey estuaries. As we pointed out earlier, the collections of small juveniles (30–50 mm, Fig. 4) occurred in a single year (1975) but not in subsequent years (1976–80). In addition, small juveniles are rarely encountered in the winter (January–April), following recruitment to the estuary (Fig. 4). Limited data might lead to the assumption that YOY *P. dentatus* could not survive winter temperatures in New Jersey inshore waters. Johns et al. (1981) indicate that larval *P. dentatus* fail to develop past yolksac absorption when reared at temperatures below 5°C. Estuarine temperatures in New Jersey regularly drop to several degrees below this level in winter (Rutgers Univ., Mar. Field Stn., Tuckerton, NJ 08067, unpublished data). Thus, if transforming individuals suffer the same mortality as the yolksac larvae, individuals that have moved into the estuaries may not survive winter. Also, several studies indicate that *P. dentatus* in Chesapeake Bay may succumb to infections of the hemoflagellate *Trypanoplasma bullocki* at low temperatures (Burreson and Zwerner 1982, 1984; Sypek and Burreson 1983). Effective immune response to the parasite was not noted in natural infections below 10°C (Sypek and Burreson 1983). This parasite occurs in New Jersey waters (G. Burreson, Va. Inst. Mar. Sci., Gloucester Pt., VA 23062, pers. commun. July 1987), but its effect on New Jersey populations of *P. dentatus* is unknown.

Some authors have assumed that because of the perceived paucity of YOY in New Jersey and other estuaries in the northeastern United States, the important nurseries for *P. dentatus* occur in Virginia and North Carolina (see Rogers and Van Den Avyle 1983 for review). We find the evidence to support this conclusion ambiguous and in some cases contradictory. First, the evidence for abundant juvenile *P. dentatus* is based primarily on studies in South Atlantic Bight estuaries that no doubt support *P. dentatus* nurseries (Tagatz and Dudley 1961, Miller and Jorgenson 1969, Burns 1974, Powell 1974, Cain and Dean 1976, Bozeman and Dean 1980). However, some of these data sources (Weinstein 1979, Weinstein et al. 1980) also include southern flounder *P. lethostigma* and gulf flounder *P. albigutta*, but the patterns observed are considered characteristic of *P. dentatus* (see Rogers and Van Den Avyle 1983). Second, there is evidence that estuaries in the northern Mid-Atlantic Bight do provide nurseries for juvenile *P. dentatus* (Grosslein and Azarovitz 1982). This has been substantiated for Connecticut (Pearcy and Richards 1962), Long Island (Poole 1961), New Jersey (Table 1 and this study), Delaware Bay (this study), and coastal Delaware (Pacheco and Grant 1973). That nurseries occur in these areas would certainly be consistent with the extensive spawning and larval development that occur in the northern Mid-Atlantic Bight (Smith 1973 and this study), especially considering the lack of evidence for larval transport or advection from this area. Third, the habitats utilized by small juvenile flounder may be difficult to sample. There is evidence that juvenile *P. dentatus* use eelgrass beds in North Carolina (Adams 1976), Chesapeake Bay (Orth and Heck 1980, Weinstein and Brooks 1983) and New Jersey (senior author's pers. observ.). Sampling flatfishes in these structurally complex habitats with conventional gears (trawls, seines) is inefficient and difficult.

To our knowledge, no one has presented data to confirm or deny the possibility that *P. dentatus* uses the continental shelf as a nursery area. Certainly spawning in the Mid-Atlantic Bight and on Georges Bank occurs great distances from estuaries (Fig. 2). Perhaps many of the larvae undergo transformation, descend to the bottom over the continental shelf, and then move into estuarine areas at a variety of sizes, beginning with early transforming individuals. This could help explain the relative scarcity of small juveniles and the large numbers of YOY (150–320 mm) that appear during summer (Fig. 4). These YOY occur in the recreational fishery in New Jersey in some years (Festa 1979). A continental shelf nursery area is more tenable in the northern Mid-Atlantic Bight, given the broad continental shelf (~150 km) relative to the narrow shelf (~50 km) off North Carolina. We know of no adequate continental-shelf sampling program, using appropriate collecting gear, to support or refute this possibility, but suggest it should be vigorously tested.

The growth of YOY *P. dentatus* in New Jersey estuaries appears to be very fast, with individuals reaching 160–320 mm 1 year after spawning (October, Fig. 4). An almost identical growth rate has been found in Long Island estuaries (Poole 1961), where length frequencies reported for July, August, and September are similar to those from New Jersey (Fig. 4). Additionally, the modal sizes of males (25.1 cm) and females (27.1 cm) of YOY reported from Long Island (Poole 1961) and those for both sexes from New Jersey (Fig. 4) are similar to the modes of YOY captured in fall over the continental shelf (Fig. 5). Assuming little or no

growth during winter, these lengths would approximate those of individuals that are forming the first annulus during the winter. Similarly, a laboratory study of *P. dentatus* collected from North Carolina found a mean size of 232.8 mm TL at the end of 1 year under constant conditions, although most growth occurred June–November (Klein-MacPhee 1979).

Earlier attempts to review the age and growth of *P. dentatus* along the east coast of the United States (Smith et al. 1981) were not completely successful because of variation in size at first annulus formation. Our data support the estimates of size at first annulus formation proposed by Poole (1961), an interpretation that was not accepted by those at the age and growth workshop (Smith et al. 1981). The latter favored a slower growth estimate based on data from North Carolina estuaries (Powell 1974, 1982).

An alternate interpretation of the available *P. dentatus* growth data, and one that would resolve the above discrepancy, is that YOY *P. dentatus* from New Jersey grow at a faster rate than do those from North Carolina. This is consistent with the workshop interpretation that overall fish growth rate tended to increase from south to north (Smith et al. 1981) and with the presence of larger YOY individuals in more northern fall collections (Fig. 7). The possibility of geographical differences in growth patterns is also consistent with the view that northern Mid-Atlantic Bight populations of *P. dentatus* are distinct from those south of Cape Hatteras (Wilk et al. 1980, Delaney 1986).

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Inferring Demographic Processes from Size-Frequency Distributions: Simple Models Indicate Specific Patterns of Growth and Mortality

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Abstract.– Models used by fisheries managers and population ecologists to analyze or predict the size-frequency distribution of populations usually incorporate assumptions concerning recruitment, mortality, and individual growth that provide mathematical simplicity, but also constrain the shapes of size distributions. In this paper we derive a predictive model for size-frequency distributions which assumes constant recruitment and mortality, and Brody-Bertalanffy growth, then examine the effects of specific violations of these assumptions on the potential shapes of size distributions. Although bimodal and strongly unimodal size-frequency distributions are not possible under these assumptions, the model indicates that specific age-related changes in the mortality rate (Z) and the growth coefficient (K) are required to obtain these distributions. Shifts in Z/K with age from growth-dominated ($Z/K<1$) to mortality-dominated ($Z/K>1$) usually result in strongly unimodal size-frequency distributions. Stable bimodal distributions require shifts from mortality-dominated to growth-dominated conditions via age-related changes in Z, K, or both. Non-equilibrium conditions or events such as pulses in recruitment or mortality can also modify size-frequency distributions, but these effects are usually transient. These results indicate that inferences concerning the demographic dynamics of a population may be derived simply by observing the shape of its size-frequency distribution.

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Population ecologists and wildlife managers are often interested in identifying spatial and temporal patterns of growth and mortality in order to understand the dynamics of populations. Because of logistic or other constraints in their abilities to directly quantify mortality and growth, however, ecologists often rely on the analysis of size distributions to infer these parameters (Cassie 1954; Beverton and Holt 1956; Ricker 1958, 1975; Ebert 1973; Van Sickle 1977b; Pauly and Morgan 1987). A population's size-frequency distribution (hereafter referred to as size distribution or size structure) results from its recent history of recruitment and mortality, integrated with the growth rates of individuals. Temporal or spatial changes in the size structure of a population must therefore reflect changes in one or more of these parameters. For example, red sea urchins *Strongylocentrotus franciscanus* are long-lived and have size distributions that are relatively stable through time, but vary in space due to geographic changes in recruitment and mortality related to the distribution of predators and dispersal of larvae (Tegner and Barry Unpubl.). In some locations urchins have persistently bimodal size structures, while in others, the population is unimodal or amodal.

Techniques for size-frequency analysis usually combine models of the growth rates of individuals with mortality rates to describe observed size-frequency distributions. Because growth and mortality both affect the shape of the distribution, knowledge of one parameter may allow deduction of the other from the shape of the size-frequency distribution. Since growth, mortality, and recruitment can vary considerably, as well as independently of one another, analyses of size distributions typically utilize several simplifying assumptions.

In this paper, we show that although simplified models commonly employed for growth and mortality result in a limited range of size structures, they can nonetheless be indicative of the demographic patterns of populations. Thus, examination of size-frequency distributions may allow reasonable inferences concerning the dynamics of a population. In particular, bimodal size distributions, that are "impossible" under typical model assumptions but are typical of red urchins in the Southern California Bight, must arise from particular patterns of age or size-specific changes in demographic parameters. In order to generate these size structures, assumptions concerning constant mortality and growth coefficients are not tenable.

The most basic assumption of most models is that the population is stable and has a stationary age structure. Thus, recruitment is taken to be invariant from year to year, or continuous, and mortality rates are presumed

constant over time. In addition to these assumptions, the population is usually required to conform to strictly deterministic equations that describe growth and abundance. Often, mortality rate is also assumed to be independent of age (Green 1970, Ebert 1973), resulting in a type II survivorship curve (Deevey 1947). Growth rates of individuals are frequently assumed to fit a Brody-Bertalanffy function (von Bertalanffy 1957, Ricker 1975) in which size increases at a rate proportional to the distance from the maximum size. For models in which one or another of these assumptions is relaxed, see Van Sickle (1977a,b), DeAngelis and Mattice (1979), DeAngelis and Coutant (1982), and several papers in Pauly and Morgan (1987).

The applicability of these simplifying assumptions varies considerably among species and populations. For some species (e.g., certain long-lived fishes of arctic lakes), age structures are stable and size distributions are stationary, with fairly constant recruitment from year to year (Johnson 1976). For many species, however, the assumption of a stable age structure is unrealistic, due to considerable interannual variability in recruitment to the zero age class (Johnson et al. 1986, Pearse and Hines 1987, Raymond and Scheibling 1987, Barry 1989). For red urchins, although recruitment varies between years, the shape of its size distribution is characteristically constant from year to year (Tegner and Barry Unpubl.). The assumption of an age-invariant mortality rate is also probably unwarranted for many, if not, most species. A more common pattern is high juvenile mortality, followed by high adult survival (type III survivorship). Models incorporating these simplifying, but perhaps unrealistic, assumptions (discussed above) can, nevertheless, be of value in identifying patterns of individual growth as well as in estimating recruitment and mortality for the population. In many cases these properties may otherwise be unobtainable.

In this paper we are concerned with population dynamics that result in a bimodal distribution of sizes. Bimodal size distributions have been reported for several species, and are of considerable interest (Johnson 1976; Tegner and Dayton 1977, 1981; Shelton et al. 1979; Timmons et al. 1980; Stein and Pearcy 1982; Wilson 1983; Pollard 1985; Page 1986; Tegner and Barry Unpubl.), especially for populations that are apparently stable. Intuitively, bimodality may develop and persist under equilibrium conditions by a combination of rapid growth of individuals to adult size and high survival rates. Thus, a mode of juveniles may be distinct from an adult mode comprised of several age classes that overlap in size, with relatively few intermediate-sized, rapidly growing individuals. DeAngelis and Mattice (1979) and Power (1978) suggested that bimodality may arise from this sort of "pileup" of individuals at larger size classes due to a decrease in growth rate at adult size, even with constant mortality. Mortality decreases the number of older individuals, but a large number are left clustered near the upper size limit. Here we show that bimodal size structure must develop from particular patterns of age-specific growth, mortality, or both, that are not possible with commonly employed models. Specifically, bimodality can develop only from an increase in survivorship with age or an increase in the growth coefficient with age, or both. Even though simple models are limited in their range of size distributions, we can use these models to identify deviations from them that are necessary or sufficient to produce particular size distributions, such as bimodal or strongly unimodal distributions.

Derivation of a simple size-frequency model

The change in abundance of a cohort can be represented as,

$$\frac{dN}{dt} = -ZN \tag{1}$$

where N is the number of individuals alive in the cohort at time t, and Z is the instantaneous mortality rate for the population. Assuming that Z is constant over time and independent of age and size, this equation can be integrated to obtain a simple decreasing exponential function for the number of individuals versus time,

$$N_t = N_0 e^{-Z(t-t_0)} \tag{2}$$

where t_0 is the time of recruitment or birth and N_0 is the abundance of the population at time t_0. The equation can be simplified slightly by defining abundance in terms of age rather than time; age (τ) equals $t-t_0$, or time since recruitment. Hence, equation (2) becomes

$$N_\tau = N_0 e^{-Z\tau}. \tag{3}$$

If we now assume that the population is stable, with constant recruitment, this function describes both the time series of abundance for a single cohort and the stable age structure of the population.

Brody-Bertalanffy growth is characterized by exponentially decaying growth in size, with no lag during early life. The general form of this deterministic equation is

$$S_t = S_\infty(1 - be^{-k(t-t_0)}) \tag{4}$$

where S_t is the size of an individual at age τ (i.e., at time t after t_0, the time of birth or recruitment), S_∞ is

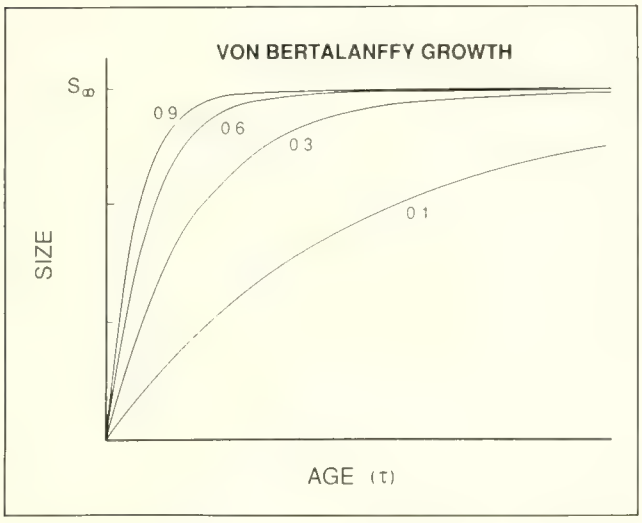

Figure 1
Brody-Bertalanffy growth for various values of the Brody growth coefficient K. Values of K are listed adjacent to each curve.

the maximum size, b is a scaling factor to account for a size at recruitment larger than 0 (for a recruitment size of 0, $b = 1$), and K is the Brody growth coefficient (Ricker 1975) which constrains the shape of the function. Higher values of K result in a more rapid approach to asymptotic size (Fig. 1). If b is considered to be unity and age (τ) rather than time is used, the equation simplifies to

$$S_\tau = S_\infty (1 - be^{-K\tau}). \tag{5}$$

Assuming these functions adequately describe the mortality and growth schedules of the population, we can combine equations (3) and (5) to derive an expression for the size-frequency distribution of the population. By definition, the number of individuals alive in an age interval τ_1 to τ_2 in equation (3) is equal to the number in the corresponding size interval S_1 to S_2, as determined by equation (5).

$$N_S \, d\tau = N_\tau \, dS_\tau$$

and rearranging,

$$N_S = N_\tau \frac{d\tau}{dS_\tau}. \tag{6}$$

Because we assume these relationships to be strictly deterministic, we can solve equation (5) for τ

$$\tau = -\frac{1}{K} \ln\left(1 - \frac{S_\tau}{S_\infty}\right). \tag{7}$$

Next, we form the first derivative of equation (7) with respect to τ, yielding

$$\frac{d\tau}{dS_\tau} = \frac{1}{KS_\infty\left(1 - \frac{S_\tau}{S_\infty}\right)}. \tag{8}$$

Combining equations (6), (3), (7), and (8) yields an expression for number as a function of size,

$$N_S = N_0 e^{\frac{Z}{K}\ln\left(1-\frac{S_\tau}{S_\infty}\right)} \cdot \frac{1}{KS_\infty\left(1-\frac{S_\tau}{S_\infty}\right)}$$

which simplifies to:

$$N_S = \frac{N_0}{KS_\infty}\left(1 - \frac{S_\tau}{S_\infty}\right)^{\left(\frac{Z}{K} - 1\right)}. \tag{9}$$

This size distribution function (9) describes population abundance as a function of size, rather than age, for any conditions of constant mortality (Z) and growth coefficient (K). By evaluating its first derivative at $dN/dS = 0$, we can identify conditions necessary for the existence of a zero slope (modes or troughs) in the size distribution. This derivative is

$$\frac{dN}{dS} = \frac{N_0}{KS_\infty}\left(\frac{Z}{K} - 1\right)\left(1 - \frac{S_\tau}{S_\infty}\right)^{\left(\frac{Z}{K} - 2\right)}\left(-\frac{1}{S_\infty}\right)$$

$$= \left(\frac{Z}{K} - 1\right)\frac{-N_0}{KS_\infty^2}\left(1 - \frac{S_\tau}{S_\infty}\right)^{\left(\frac{Z}{K} - 2\right)}. \tag{10}$$

The conditions where $dN/ds = 0$ are:

$N_0 = 0$: trivial
$S_\tau = S_\infty$: trivial
$S_\infty = \infty$: trivial
$Z = K$: growth is balanced by mortality.

The only non-trivial condition where the size-frequency function has a slope of zero is when $Z = K$. In this case all size classes are equally abundant, since the solution to equation (9) indicates that when $Z = K$, N_S is constant and independent of S_τ. Therefore, there are no conditions of growth and mortality that are capable of producing a bimodal distribution when using these simplifying assumptions. Thus, the hypothesis that bimodality arises from rapid growth to adult size

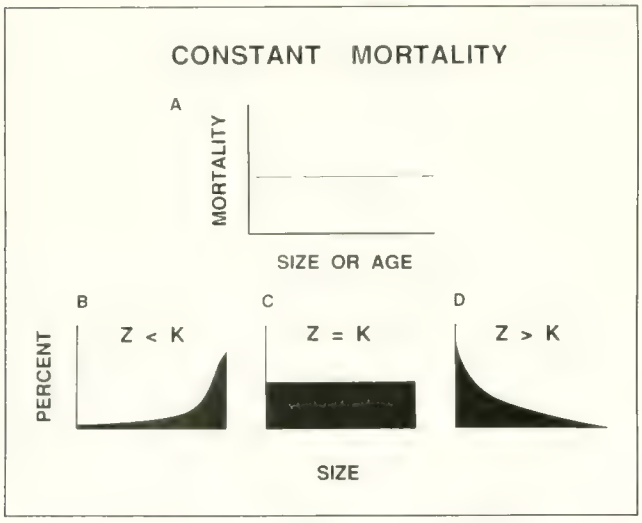

Figure 2

Hypothetical size-frequency distributions for populations exhibiting constant mortality and von Bertalanffy growth. (A) Mortality (Z) is constant for all sizes. The growth coefficient (K) is also assumed to be a constant. Due to these assumptions, the shape of size-frequency distributions are limited to those general forms presented in b–d, according to the relative magnitudes of Z and K. (B) Z is less than K over all S. (C) Z equals K. (D) Z is greater than K.

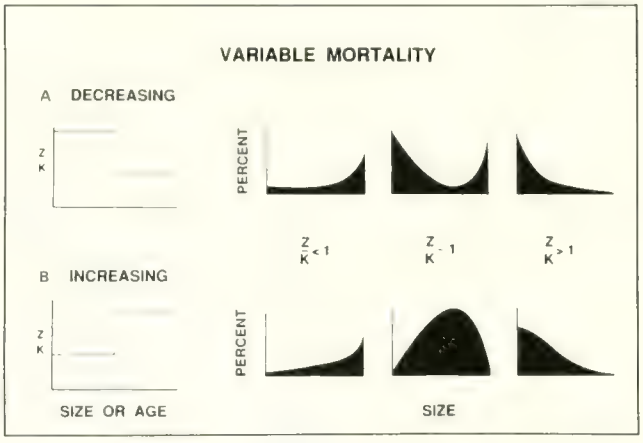

Figure 3

If the assumptions of constancy for Z and K are violated, the shape of a size distribution varies according to the pattern of the violation. The figures on the left-hand column indicate a shift (step function) in the relative values of Z and K, with age or size. The figures in the three right columns show the general shape of the size-frequency distribution for the specified conditions, created by combining the predicted size distributions for before and after the change in K or Z. (Row A) For a decrease in the ratio of Z/K with larger size, bimodality is possible, depending upon the magnitude of Z and K. When Z is near in value to K, and Z/K shifts from greater than to less than unity, bimodality is likely. For cases where Z is always greater than K or less than K, the size-frequency distribution is dominated by juveniles, or adults, respectively. (Row B) For an increase in Z/K, the size distribution may be unimodal with a mode in any position, but cannot be bimodal. For each of the three right columns, the appropriate value of Z/K for the interval S_0 to S_∞ is indicated.

and high (constant) survivorship (Van Sickle 1977a, Power 1978, DeAngelis and Mattice 1979), is not adequate, assuming simple Brody-Bertalanffy growth and constant mortality under steady-state conditions. There must be a more complicated age dependence of growth rate, or an age dependence of mortality, to account for a bimodal stable size distribution.

Because the signs of N_0, S_τ, S_∞, and K are all positive, the sign of dN/dS in equation (10) is determined by the first term (Z/K-1). If Z is greater than K, the slope is negative and the size structure is dominated by juveniles (Fig. 2). When Z is less than K, the slope is positive, up to S_∞, and the population is dominated by adults. These can be termed mortality-dominated and growth-dominated populations, respectively.

Effects of age-related rates of growth and mortality

Let us now relax the assumption that K and Z are independent of age. Age-specific variation in these coefficients can result in a bimodal or unimodal size distribution, depending upon the relative magnitude of K and Z. The derivations of similar models for age-varying K and Z are more complicated, but we can evaluate the effect of such changes simply by considering a combination of size distributions generated with different values for one or both of these coefficients. The important implications remain unchanged. If K or Z changes with size such that the ratio of Z/K shifts from greater than to less than unity as size increases, the slope of the size distribution will change from negative to positive: conditions required for a bimodal distribution (Fig. 3). In contrast, a shift from growth-dominated ($Z/K<1$) to mortality-dominated ($Z/K>1$) conditions produces a strongly unimodal pattern, with the position of the mode determined by the size where $Z = K$.

Obviously, variation in the ratio of Z/K can arise from size or age-specific changes in the value of Z, K, or both. Although Bertalanffy-type growth curves assume K to be independent of age, the growth intervals of species are frequently shown to exhibit variations in K with age, with K commonly decreasing slightly with age (Ricker 1975). For example, decreases in K with size or age are evident from the increasing slope of Walford plots for sea urchins *Strongylocentrotus purpuratus* presented by Russell (1987). Estimates of K from Russell's Figure 3 decrease from approximately 0.5 to 0.05 from small to large urchins at most locations. Assum-

ing the reported instantaneous mortality rates ($Z \approx 0.1$) to be constant, the age-specific Z/K ratio indicates that the size-specific population dynamics switch from growth-dominated ($Z/K<1$) to mortality-dominated ($Z/K>1$), which might account for the observed strongly unimodal size-frequency distributions. Other species of urchins (Tegner and Dayton 1977, 1981; Himmelman 1986; Tegner and Barry Unpubl.) as well as many species of long-lived arctic fishes (DeAngelis and Mattice 1979) exhibit bimodal size-frequency distributions and must, under steady-state conditions, undergo a shift from mortality-dominated to growth-dominated population dynamics.

In that the growth rates of individuals usually decrease with age (Ricker 1975, but see Campbell 1979, Himmelman 1986), the most likely cause of persistently bimodal size distributions under steady-state conditions is an even greater decrease in the mortality rate of large individuals. A reduction in mortality, assuming a constant or slightly decreasing growth coefficient, could allow Z/K to shift from >1 to <1: conditions necessary for bimodality.

Evidence for lower mortality with larger size or age is common. Many species exhibit type III survivorship curves of decreasing mortality with age (Deevey 1947, Odum 1971, Wilson and Bossert 1971). For example, because lobsters preferentially consumed small-sized red urchins *Strongylocentrotus franciscanus* (Tegner and Levin 1983) and sheephead *Semicossyphus pulcher* repeatedly select smaller *S. franciscanus* when offered a choice of sizes (Tegner and Dayton 1981), predation mortality apparently decreases with size (= age) in urchins. In addition, geographic differences in the size structure of red urchins are related to the distribution of predators, with bimodal size-frequency distributions found where these predators are most abundant (Tegner and Barry Unpubl.). Intraspecific competition for resources and high adult survivorship appear to limit the growth or survival rates of juveniles or both for arctic fishes (Johnson 1976), green sea urchins (Himmelman 1986), as well as forest trees (Harper 1977), often leading to a bimodal distribution of sizes; however, bimodality in these populations may arise from stochastic, age-specific changes in growth (DeAngelis and Coutant 1982).

Unstable or non-equilibrium conditions

There are conspicuous alternative causes of bimodal size-frequency structures for populations with unstable or non-stationary age compositions. In particular, species that have seasonal recruitment and live for only two years (e.g., blue crabs; Hines et al. 1987) have persistent, but recruitment-controlled bimodality. For longer-lived species, relaxation of the assumptions of a stable age structure and stationary size distribution allow for transient, but perhaps persistent, variations in age and size structures due to temporal variation in recruitment and mortality. Interannual variation in recruitment, to a population normally dominated by an adult mode, can skew the age structure and occasionally produce a mode of juveniles, thereby resulting in bimodality. This feature will, however, deteriorate as the juveniles grow and merge into the adult mode. Similarly, a mortality-dominated population can become bimodal when a large pulse of juveniles grows to adult size, before being eventually depleted by mortality. In both cases bimodality is a transient feature of the size structure. How long it will persist is determined by the rapidity with which individuals grow to asymptotic size as well as the range of variation in recruitment. Recruitment pulses leading to unstable size and age distributions have been reported for several species (Hjort 1914, 1926; Ebert 1983; Cowen 1985; Johnson et al. 1986; Paine 1986; Pearse and Hines 1987; Raymond and Scheibling 1987).

Variation in growth and mortality within an age cohort, due to stochastic processes and genetic variability, can disrupt the deterministic character of growth and survivorship processes leading to a highly variable age and size structure, even within a single cohort. Intraspecific competition for resources can induce bimodality within a single cohort if growth to a particular size confers a great competitive advantage, leading to even more rapid growth (DeAngelis and Coutant 1982). For example, if recruitment by juveniles into the adult size classes is regulated by stochastic processes that provide limiting resources to a few juveniles upon the removal of adult individuals, the size structure of a cohort may become bimodal. This is apparently typical of arctic fishes (Johnson 1976), largemouth bass (Shelton et al. 1979; Timmons et al. 1980), green sea urchins (Himmelman 1986), stalked barnacles (Page 1986), and many species of forest trees (Harper 1977).

Value of simple size-frequency distribution models

As shown in this analysis, even very simple models of size-frequency distributions, with perhaps unrealistic assumptions, can provide valuable information concerning the growth and mortality schedules of populations. Although the range of potential size structures is constrained by model assumptions such that bimodal size distributions, or unimodal distributions with the mode centered away from S_0 or S_∞, are not possible, we can still utilize these models to identify likely

patterns of age-related mortality and growth; "impossible" size-frequency distributions are indicative of specific violations of the assumptions. Even though model assumptions impose severe restrictions upon the shape of size distributions, the shape of an observed distribution, coupled with marginal information concerning recruitment and growth for the species, can be used to infer age-related changes in growth, mortality, or both, leading to better directed research efforts on the population. This is particularly important for species such as red urchins which show strong geographical variation in their population dynamics (Tegner and Barry Unpubl.); fishery managers often must rely on easily collected size-frequency information to infer demographic parameters, rather than costly population studies at several locations.

Acknowledgments

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Abstract.– Three cohorts of *Penaeus indicus* were sampled with a beam trawl at 6-week intervals over 2 years in the St. Lucia Lake system. Shrimp recruited to the system over September–November (spring) and March–May (autumn) and overwintered in the estuary. Mean growth rates of cohorts over the size range 7.25–17.66 mm carapace length (CL) ranged from 0.032 to 0.058 mm CL per day with the autumn cohorts exhibiting the slowest growth and longest residency times. Up to 26.5°C, growth rates were positively correlated with water temperature. Growth was negligible at temperatures between 19 and 22°C. Shrimp emigrated from the estuary between the sizes of 18 to 25 mm CL. The onset of emigration appeared to be related to declining water temperatures.

Growth and Emigration of *Penaeus indicus* H. Milne-Edwards (Crustacea:Decapoda:Penaeidae) in the St. Lucia Estuary, Southern Africa

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The commercial importance of penaeid shrimp is well documented with 1987 United States commercial landings valued in excess of $515 million (U.S. Department of Commerce 1988). Shrimp fisheries in the Indo-Pacific region generate considerable revenue, and India is the region's major shrimp supplier. *Penaeus indicus* H. Milne-Edwards, 1837 is numerically the most important species in the Indian shrimp fishery (Silas et al. 1984) and likely formed the majority of the $56.9 million of shrimp exported to the United States by India in 1987 (U.S. Department of Commerce 1988).

The distribution of *P. indicus* extends along the east African coast into the inshore waters of Natal, South Africa (Champion 1983). In common with many inshore penaeids, it utilizes estuaries during the juvenile phase of its life cycle and migrates offshore for subsequent maturation and reproduction (Garcia and Le Reste 1981). The proximity of St. Lucia to the southern limit of distribution of this essentially tropical species suggested the desirability of investigating the relationship between the growth of *P. indicus* and temperature as well as the factors responsible for onset of offshore emigration.

The St. Lucia Lake system is the largest estuary in southern Africa and provides a nursery habitat for *P. indicus* and several other penaeid species (Joubert and Davies 1966, Forbes and Benfield 1986a). The Natal Parks Board has operated a bait fishery for shrimp in the system since 1952 (Joubert and Davies 1966), with annual landings of approximately 16 t. *Penaeus indicus* typically constitutes 80–90% of this catch (Forbes and Benfield 1986a). An offshore South African commercial fishery also depends largely on *P. indicus* (Forbes and Benfield 1985).

Most penaeid shrimp exhibit rapid growth which is frequently correlated with water temperature. Little information is available on the growth of the St. Lucia penaeids. Joubert and Davies (1966) conducted four surveys over a 1-year period and provided estimates of growth for *P. indicus* and two other numerically

important penaeids. However, their sampling frequency was too low to follow the growth of individual cohorts or identify principal periods of emigration from the system.

While the timing of shrimp emigration from estuaries varies with species and geographic area, a number of factors have been suggested as causal stimuli. These include declines in temperature (Lindner and Anderson 1956, Pullen and Trent 1969, Chen 1983, Matylewich and Mundy 1985), declines in salinity (Rothlisberg et al. 1985, Staples and Vance 1986, Jayakody and Costa 1988), increased tidal amplitude and currents (Copeland 1965), and an endogenous rhythm coupled with tidal currents (Hughes 1972).

This study was initiated to provide information about the growth and emigration of *P. indicus* in St. Lucia and operated concurrently with a plankton sampling program that provided information about the immigration of *P. indicus* postlarvae (Forbes and Benfield 1986b). The present paper contains estimates of seasonal differences in growth rates and periods of emigration for *P. indicus*.

Methods

Beam trawling

Sampling was conducted in South Lake and the St. Lucia Narrows, a 21-km channel connecting the lakes with the Indian Ocean; twelve sampling stations were selected (Fig. 1). Samples were collected 17 August 1982–6 November 1984 at 4–6 week intervals coincident with spring tides and the plankton sampling program. Sampling during the first half of 1984 was disrupted when a cyclone struck at the end of January and cut off access to the area. A single sample was obtained in April and routine sampling resumed in July 1984.

A 1-m beam trawl with a frontal area of 0.3 m^2 was attached to a 12-mm stretched mesh nylon bag with 25-mm mesh nylon wings and a nylon 6-mm mesh cod. The bag was fitted with a floating headrope, weighted baserope, and a tickler chain. The trawl was towed 6 m behind an open boat fitted with two outboard engines. At each site, a 10-min trawl was taken against tidal flow (where present) parallel to, and within 10 m, of the shore. Tow distances were not measured but were probably similar because tidal currents were generally weak in the vicinity of the sampling stations. Catches were frozen and returned to the laboratory where species, sex, and carapace length were determined. Water temperatures were recorded mid-trawl at each station.

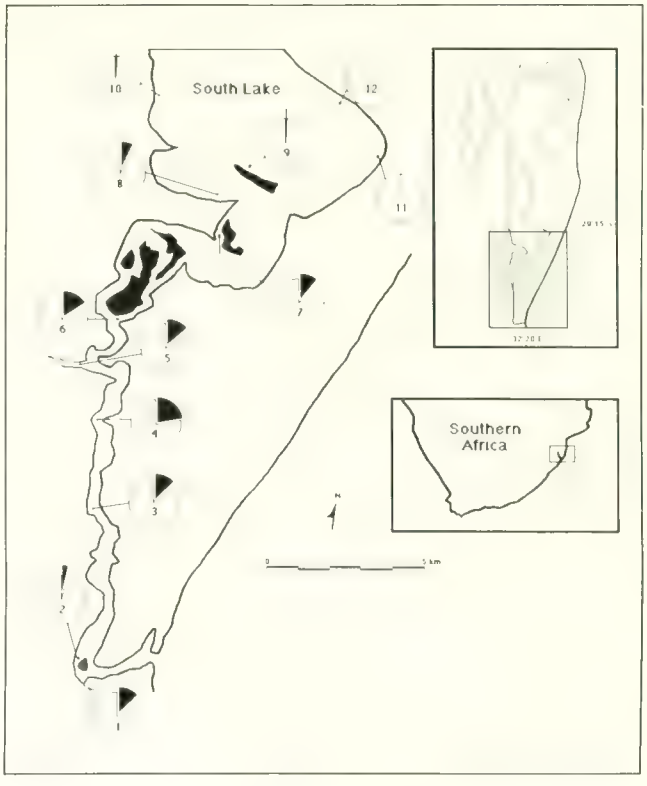

Figure 1
Sampling stations in the St. Lucia Lake system. Pie charts indicate the contribution of each sampling station to the total beam trawl catch of *Penaeus indicus*.

Bait fishery

A bait fishery operates throughout the Narrows (vicinity of stations 1–7) and in lower South Lake (vicinity of stations 8–10) and employs 3.7-m gate trawls with a frontal area of 3.45 m^2 and a 25.4-mm stretched mesh bag. Frozen samples, provided at irregular intervals of several days to several months between 17 September 1982 and 2 April 1985, were treated in the same manner as the beam trawl samples.

Data analysis

The beam trawl length-frequency data from all sites were pooled because sample size differences among sites were frequently large, and the sample sizes from individual sites were often too small to construct meaningful length-frequency histograms. A computer program (MIX) (MacDonald 1986) was used to fit normal curves to the component cohorts in each distribution. Growth rates were estimated by following the mean size of the youngest cohort over consecutive sampling periods. Older cohorts were excluded from the analysis because of the confounding effect of emigration on the cohort mean. The appearance of a new cohort in the

beam trawl catch was related to prior pulses of postlarvae in the plankton. Over this interval, the growth rate was estimated by relating the mean size of postlarvae to the mean size of the subsequent cohort of juveniles in the beam trawl catch.

Length-frequency histograms were constructed from the sum of all shrimp caught over the entire sampling period for the beam trawl and bait fishery samples. These two histograms were used to estimate the approximate size of shrimp at the onset of emigration. Declines in the frequency of shrimp within the emigrating size classes over successive sampling intervals were used to identify possible periods of emigration.

Results

Distribution and abundance

Shrimp were captured throughout the Narrows and in limited numbers along the western shore of South Lake. Five specimens were taken along the eastern shore (station 11). Catches were highest in the middle Narrows (stations 4–6) and declined in either direction from that section (Fig. 1).

Shrimp concentrated in the middle Narrows for most of the year with some seaward shift in their distribution evident December–February (summer) (Fig. 2). The apparent shift towards the lower Narrows during June–August (winter) is a consequence of the capture of large numbers of 7–12 mm CL shrimp at station 1 in August 1983 (Fig. 2).

Juvenile shrimp were present throughout the year, declining over January–February (late summer) toward a March–May (autumn) minimum and increasing during June–November (winter and spring) (Fig. 3).

A substantial proportion of the *P. indicus* population was presumed to have been washed out of the system during the January 1984 cyclone. During the months following the cyclone, shrimp numbers increased slowly, and by July 1984 shrimp were sufficiently abundant for the bait fishery to resume operation. Beam trawl sample sizes remained too low to adequately define the population structure, and growth estimates could not be provided for the post-cyclone samples.

Growth

Growth rates were estimated over the size range 1.72–20.12 mm CL for three cohorts that entered the system prior to the cyclone (Fig. 4). These estimates ranges from 0.0005 to 0.1634 mm CL per day. Cohort 1 exhibited approximately linear growth up to 13.92 mm CL (Fig. 4) and had a mean growth rate of 0.058 mm CL per day over the size range 7.25–13.92 mm CL. Cohort 2 displayed a pronounced seasonal fluctuation

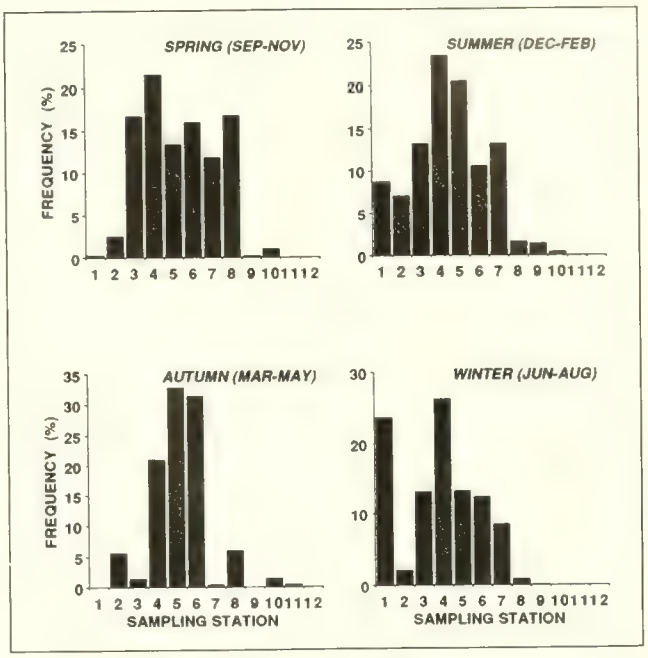

Figure 2

Mean seasonal distribution of *Penaeus indicus* in the St. Lucia system. See Figure 1 for sampling station locations

in its growth pattern (Fig. 4). The mean growth rate of this cohort was 0.035 mm CL per day over the size range 8.99–17.66 mm CL. Cohort 3 also displayed seasonal fluctuation in its growth. The mean growth of this cohort was 0.040 mm CL per day over the size range 8.83–14.81 mm CL.

For the size range 7.25–17.66 mm CL, growth was significantly correlated with the mean water temperature of each sampling interval (Spearman's coefficient of rank correlation $r_s = 0.746$, $t = 3.361$, 9 df, $p<0.01$) (Fig. 5). This response was particularly evident in cohorts 2 and 3 which showed a pronounced decline in their growth during the cooler winter months (Fig. 4). Cohort 1 also overwintered and probably followed a similar pattern while it was too small to be effectively sampled by our gear.

Emigration

The first cohort entered the system during early May 1982 and emigrated over January–March 1983. A second cohort which may have recruited during early summer 1982 emigrated over December 1983 and January 1984. Emigration of the third cohort, which entered in April 1983, may have been prematurely initiated by the cyclone at the end of January 1984. Two cohorts thus entered the system during April–May (autumn) with possible recruitment during November–December (early summer) by the remaining cohort. All

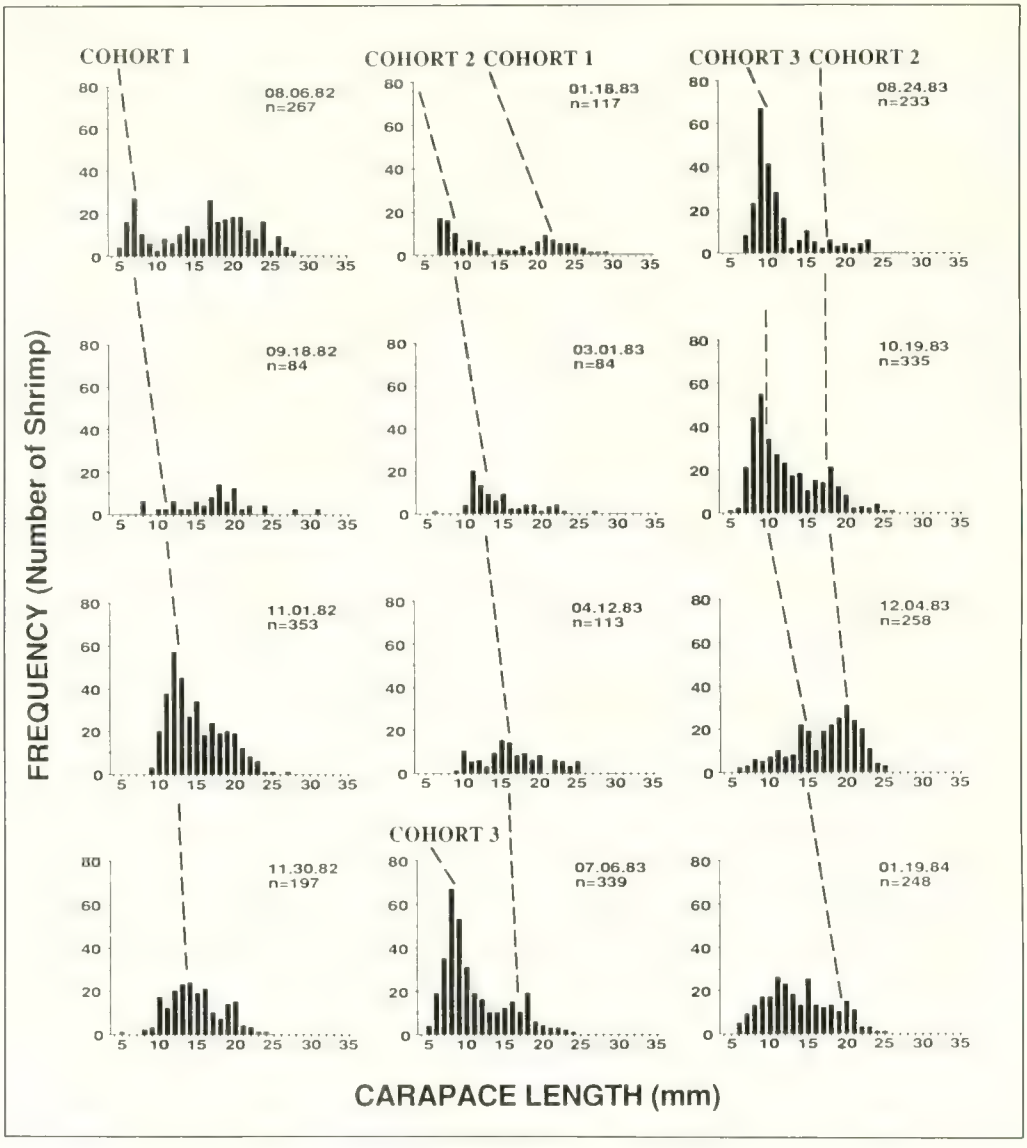

Figure 3

Length frequency histograms for three cohorts of *Penaeus indicus* in the St. Lucia system between 6 August 1982 and 19 January 1984. Dashed lines indicate positions of fitted cohort means.

three cohorts overwintered in the estuary and emigrated during December–March (summer–autumn).

Penaeus indicus began to leave the system upon attaining approximately 18 mm CL with most emigration occurring between 20 and 25 mm CL (Fig. 6). Declines in the proportions of 20–25 mm CL shrimp in both the beam trawl (Fig. 3) and bait fishery samples (Fig. 7) supported the December–May (summer–autumn) emigration hypothesis. Emigrating size classes declined sharply in the baitfishery samples over April–May 1983 and January–April 1985 (Fig. 7).

Emigration did not appear to be related to salinity fluctuations. The wet and dry seasons are not well defined in St. Lucia, which receives 62% of its annual precipitation (1971–81 data for the estuary mouth, Natal Parks Board, unpubl.) during summer and autumn when most emigration appears to occur. During our study period, salinities in the lower Narrows showed little fluctuation during the emigration of the first cohort, but did decline prior to and during the emigration of the second (Fig. 4).

A more convincing relationship exists between emigration and declining water temperatures. Water temperatures decreased during the emigration of cohort 1 (Figs. 4 and 7) and may have begun to cool by the onset of emigration in the second cohort. The

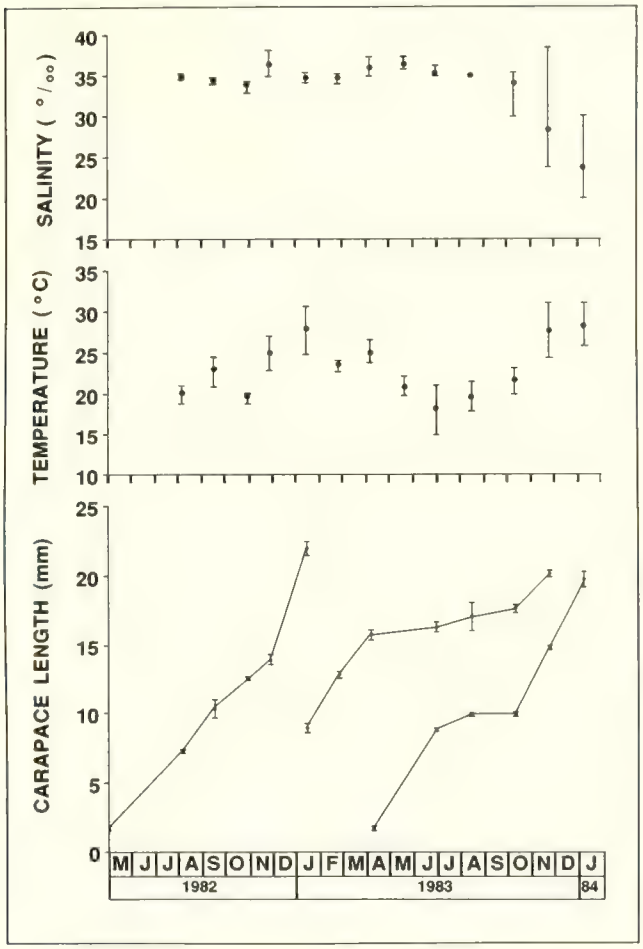

Figure 4

Mean carapace length of *Penaeus indicus* cohorts in the St. Lucia system over time; vertical bars indicate 1 standard deviation. Upper scales indicate corresponding mean temperatures and salinities averaged across sampling stations 1–7; vertical bars indicate maxima and minima.

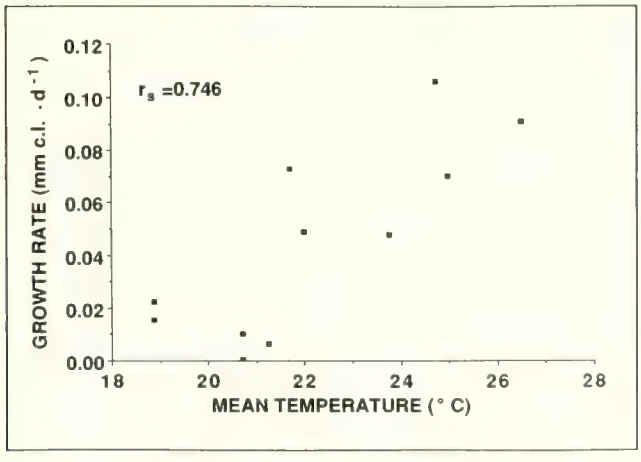

Figure 5

Relationship between growth rates of *Penaeus indicus* (7.25–17.66 mm CL) and corresponding mean water temperatures in the St. Lucia system determined for consecutive sampling intervals.

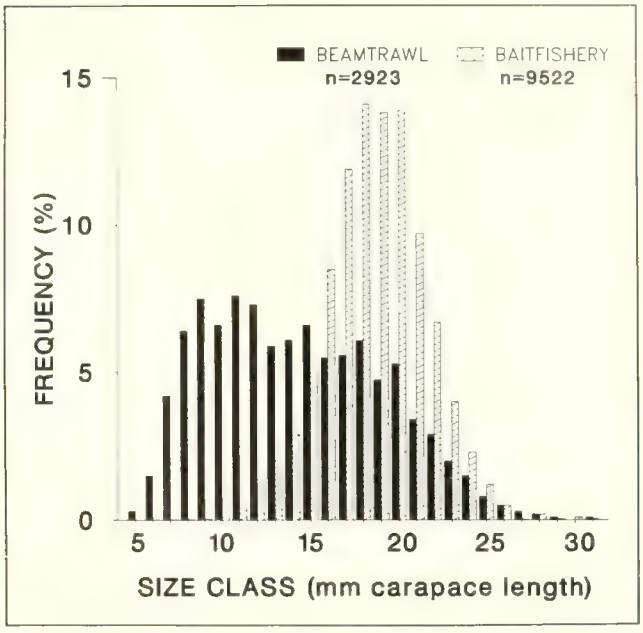

Figure 6

Cumulative length-frequency histogram of *Penaeus indicus* for beam trawl (August 1982–November 1984) and bait fishery (September 1982–August 1985) in the St. Lucia system. Plot truncated at 30 mm CL because larger size classes contributed <0.25% of total catch.

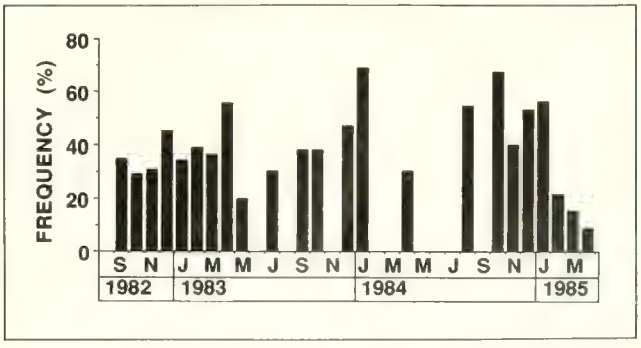

Figure 7

Monthly frequency of *Penaeus indicus* ≥20 mm CL in the baitfishery catch in the St. Lucia system. Blank intervals indicate no data available for that month.

emigration of the third cohort would likely have coincided with declining water temperatures if it had not been forced by the cyclone.

Discussion

Estimation of growth rates and emigration size depend on a representative sample of the population at each sampling interval. Trawl samplers typically have a low catch efficiency (Zimmerman et al. 1984) and a selective bias towards certain size classes (Staples 1980). Our beam trawl captured *P. indicus* over the range

4–33 mm CL. The percentage contribution by size class to the total beam trawl catch showed relatively little change between 8 and 18 mm CL (Fig. 6) suggesting that selection bias was not a problem within this range. On this basis, we are confident in using a restricted range of the catch (7–17.66 mm CL) for the growth estimates. However, our growth-rate estimates for sizes above this range may be influenced by emigration and avoidance, and should be used with caution. Similarly, the growth rates determined for small shrimp between the time of recruitment into the estuary and vulnerability to our trawl should be regarded as rough approximations because of the reduced efficiency of our gear and absence of a precise immigration time.

Growth

The mean growth-rate estimates obtained in our study are lower than those reported for *P. indicus* in other areas. This may be a consequence of the lower temperatures which prevail at the edge of this species' distribution. Parrack (1979) suggested that differences in the growth rates of *P. aztecus* populations from different latitudes could be explained by temperature differences in the bottom waters of each region. Juvenile *P. indicus* grew at 0.102 mm CL per day in Singapore ponds (Hall 1962) while Le Reste and Marcille (1976) recorded more rapid growth of 0.125 mm CL per day in Madagascar. A review of the growth rates recorded for this species (Champion 1983) suggested an average growth of 30 mm total length per month which equates to 0.176 mm CL per day when the conversion factor of Prabhakara Rao (1967) is applied and a 30-day month assumed.

Application of the von Bertalanffy growth function may be justified for some penaeid shrimp (Garcia and Le Reste 1981); however, its use is questionable in areas where growth is reduced at times by low temperatures. The reduced growth of overwintering cohorts accounts for the relatively long residency period of the shrimp in St. Lucia. Between August and October 1983, the water temperatures in the Narrows were 18–23°C. The lowest growth rates from our study occurred over 18–22°C, which may provide an estimate of the low-temperature growth threshold for *P. indicus* in St. Lucia. Comparable data for *P. indicus* were unavailable; however, our estimate of the low-temperature growth threshold is similar to estimates reported for other penaeid species. Latapie et al. (1972) found negligible growth in *P. setiferus* below 20°C, and Phares (1980) used 17°C as the zero growth temperature in a model for the same species. Below 22°C, the growth of juvenile *P. vannamei* was reduced in Mexico (Edwards 1977). In contrast, Zein-Eldin and Aldrich (1965) reported slow growth of postlarval *P. aztecus* at 18°C and a lower growth threshold of 11°C.

In several instances, the interval growth rates were inversely related to temperature. This may be a consequence of size-specific changes in growth rates overriding the effects of temperature. Hall (1962) reported linear growth up to 25 mm CL for *P. indicus*; however, there is no evidence that more complex growth models were fitted. In juvenile *P. vannamei* (Menz and Blake 1980) and juvenile *P. setiferus* (Phares 1980) growth was negatively correlated with size. While growth rates probably decline with increasing size in *P. indicus*, the observed fluctuations may also be due to changes in the thermal history of each cohort not manifested in the mean interval water temperature.

Emigration

The life cycle of *P. indicus* in St. Lucia appears to follow the generalized pattern outlined for penaeids by Garcia (1985). There appear to be two cohorts each year, the first entering during early summer and emigrating from the system over autumn and early winter; the second recruits during autumn, also overwinters in the estuary, and emigrates during the following spring and summer. A similar pattern of recruitment and emigration was observed for *P. indicus* in Singapore by Hall (1962) and in Madagascar by Le Reste (1978). This pattern has also been noted for *P. merguiensis* in Australia (Dredge 1985, Rothlisberg et al. 1985). In an earlier study of the St. Lucia penaeids, Joubert and Davies (1966) reported emigration through summer and autumn but did not indicate that this protracted emigration actually represented the overlapping departures of two cohorts.

Penaeus indicus appears to emigrate from St. Lucia and other systems over similar size ranges. In Singapore, Hall (1962) attributed a decline in the frequency of 20–25 mm CL shrimp to emigration, and in Madagascar *P. indicus* began to emigrate at approximately 20 mm CL. Prabhakara Rao (1967) suggested that *P. indicus* left Chilka Lake, India, between 18.3 and 22.9 mm CL.

Jayakody and Costa (1988) reported that *P. indicus* may emigrate from Sri Lankan estuaries in response to osmotic stress imposed by monsoon rains. The onset of emigration by *P. merguiensis* has been linked to elevated rainfall and declines in salinity (Rothlisberg et al. 1985, Staples and Vance 1986). Joubert and Davies (1966) suggested a link between migration and salinity in St. Lucia but had no experimental data to support this connection. Emigration appeared to be related to late-summer and autumn water cooling; however, the apparent correlation does not imply

causality. Other factors associated with declining water temperatures such as food availability or predation (Matylewich and Mundy 1985) may also be contributing agents.

Acknowledgments

The authors gratefully acknowledge the financial assistance of the South African National Committee for Oceanographic Research, the cooperation of the Natal Parks Game and Fish Preservation Board, D.S. Smith for construction and maintenance of sampling gear, Dr. P.D.M. MacDonald for providing access to his cohort analysis program, the Texas A&M University Computer Graphics Lab staff, and the comments of two anonymous reviewers.

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Abstract.—Exposure of developing pollock *Theragra chalcogramma* embryos to static water-soluble fractions (WSF) of Cook Inlet crude oil in seawater slowed initial development, produced shorter larvae, and caused morphological abnormalities including membranous vesicles; body curvatures; deformations of yolk, eye, brain, jaw, intestine, and pericardial sac; absence of lower jaw; fin erosion; yolksac bloating; and light pigmentation. These abnormalities were retained after hatch, and in many cases became more pronounced as developing structures failed to form properly. The median concentration of WSF that caused abnormalities (AB_{50}) was 2.1 ± 0.1 ppm. Exposure during embryonic development reduced prehatch survival by a maximum of 26%, and caused high mortality after hatch. The median lethal concentration (1.8 ± 0.6 ppm) was not significantly different than the AB_{50}. Although exposed pollock embryos generally survived to hatching, larvae were malformed, smaller, and had poorer survival potential than controls.

Abnormal Development and Growth Reductions of Pollock *Theragra chalcogramma* Embryos Exposed to Water-Soluble Fractions of Oil

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Early life stages of fish are usually more sensitive to environmental stress than adults (Moore and Dwyer 1974, Rice 1985, Carls 1987). Planktonic eggs and larvae of demersal fish, such as Atlantic cod *Gadus morhua* and walleye pollock *Theragra chalcogramma*, are generally sensitive to dissolved oil. For example, prefeeding Atlantic cod larvae grew significantly less than controls when exposed for 2 weeks to 0.07 ppm of water-soluble fractions (WSF) of Ekofisk crude oil (Tilseth et al. 1984). The frequency of oil spills is greatest near the shore where shipping and drilling activities are concentrated and navigation hazards are more frequent. For example, the oil tanker *Exxon Valdez* grounded within Prince William Sound on 23 March 1989 with disastrous consequences. Oil spilled by drilling and transportation generally concentrates in the surface layers and, therefore, may impact nearshore areas where the planktonic eggs of Atlantic cod and walleye pollock are spawned (Kühnhold 1970, Longwell 1977).

Fish embryos respond in similar ways to a broad range of stressors (Rosenthal and Alderdice 1976, Linden et al. 1980), including the WSF of crude oils. Most sublethal effects are probably biochemical in origin, and include morphological abnormalities and reductions in growth (Rosenthal and Alderdice 1976).

In this study we measured the effects of exposure to WSF hydrocarbons on the growth and development of pelagic marine walleye pollock eggs. Walleye pollock is an abundant species in the North Pacific Ocean and comprises 20–50% of the total fish biomass in the Bering Sea (Smith 1981). Pollock are ecologically and commercially important; they are a major component of the food web, and the total commercial catch off Alaska averaged 1,013,815 t during the years of this study (1982–83) (National Marine Fisheries Service 1982, 1983).

Methods

Adult walleye pollock were collected by trawling in March 1982 and May 1983 near Juneau, Alaska. Ripe adults were transported live to the Auke Bay Laboratory. Each year, eggs and milt were stripped from a single pair and mixed in a beaker without water. Eggs were then transferred at random into 15 cm diameter × 20 cm tall cylindrical glass jars wrapped with black plastic tape and each filled with 2.5 L of either hydrocarbon free seawater (28.5 ppt) or seawater contaminated with the WSF of Cook Inlet crude oil (Table 1). After a 2-hour

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Table 1

Initial concentrations of water-soluble fractions (ppm) of Cook Inlet crude oil for each treatment group of walleye pollock eggs.

	Treatment group					
	0–21 days		1–21 days		7–21 days	
Concentration	Mean	SE	Mean	SE	Mean	SE
Control	0.0		0.0		0.0	
Low	0.2	0.00	0.4	0.01	0.3	0.02
	0.6		0.8	0.02	0.7	0.10
	1.6	0.08	1.5	0.01	1.8	0.20
	2.3		2.2	0.12	2.8	0.04
Maximum	3.6	0.09	2.8	0.10	3.1	0.13

water-hardening period, all eggs were transferred to fresh seawater of the same treatments.

Fertilized eggs were exposed to five WSF concentrations, ranging from controls (0 ppm) through 3.6 ppm, beginning at day 0 (fertilization), day 1 (morula stage), or day 7 (11–14 somite stage) (Table 1). Exposures were static, and after the transfer at 2 hours, eggs remained in the same solution until hatch (approximately 21, 20, and 14 days, respectively). Larvae that hatched in the 1–21 day treatment were transferred to clean seawater immediately after hatch and observed until yolks were resorbed (~21 days). There were three replicates per concentration, with 49–101 eggs per replicate. Maximum biomass did not exceed 0.1 g/L in any replicate. Temperature was constant (3.9 ± 0.1°C). Test jars were not aerated, but oxygen was not limiting (97 ± 3% saturation at end of experiment).

Microbial growth did not cause problems. Control eggs remained healthy throughout the experiment. Any growth observed in the jars during the experiment was removed by pipette, as were dead eggs and detritus. Bacterial plates inoculated with water collected after hatch showed no significant differences between WSF and controls.

Test conditions were static, simulating a single-event oil spill, but the WSF of Cook Inlet crude oil was produced by dripping seawater through a continuously replenished 40-cm emulsified layer of oil; the resulting WSF was collected below the layer after dispersed oil floated out (Moles et al. 1985). Seawater was filtered through 5-μ glass fiber filters or approximately 10-μ sand filters before contamination with WSF. Concentrations were routinely monitored with fluorescence spectroscopy and glass-capillary-column gas chromatography as described in Carls and Rice (1988). Because polynuclear aromatic compounds were not detectable in the WSF, concentrations are reported as total mono- plus diaromatic hydrocarbons in ppm. The composition of the WSF was similar in 1982 and 1983; the principal difference was a higher percentage of naphthalene in 1983 (10.5%) than in 1982 (1.2%) (Table 2).

Table 2

Comparison of water-soluble-fraction (WSF) preparations of Cook Inlet crude oil in treatment groups of walleye pollock eggs from years 1982 (0–21 and 7–21 day treatments) and 1983 (1–21 day treatment). Concentrations of compounds in the WSF were measured by gas chromatography and converted to percentages. $n = 3$ for each compound; asterisks denote significant differences between 1982 and 1983 percentages.

	1982		1983	
Hydrocarbon	%	SE	%	SE
benzene	50.5	0.72	51.0	0.66
toluene	34.6	1.62	30.3	0.89
ethylbenzene*	2.3	0.17	0.2	0.22
m- and p-xylene	6.2	0.45	4.5	0.27
o-xylene	3.5	0.28	2.8	0.18
mesitylene*	0.6	0.15	0.1	0.03
naphthalene*	1.2	0.15	10.5	1.87
2-methylnapthalene*	0.6	0.06	0.0	0.00
1-methylnapthalene	0.5	0.02	0.3	0.12
2,6-dimethylnapthalene	0.0	0.00	0.0	0.00
1,4-dimethylnapthalene*	0.0	0.00	0.1	0.04
1,2-dimethylnapthalene*	0.0	0.00	0.2	0.04
Total mononuclear aromatics*	97.7		88.9	
Total dinuclear aromatics*	2.3		11.1	

Developing eggs were examined daily; mortality and number hatched were recorded. A few eggs (2–10/concentration · treatment) were subsampled daily for observation and measurement. Development was staged according to Yusa (1954). Blastopore diameters were measured with an ocular micrometer near the time of closure in the 1–21 day treatment. The presence or absence of morphological abnormalities was recorded. If present, the size of vesicles was coded as very small, small, medium, or large. Dead eggs were also examined for abnormalities and development stage.

Immediately after hatch, larvae were examined for abnormalities with a microscope; total body length and yolk lengths were measured with an ocular micrometer, except measurements were not made in the 1–21 day treatment. Yolk lengths were measured along the major body axis, and were considered proportional to yolk volume. Mortality and the number abnormal were counted for each replicate.

Table 3

Distribution of individual aromatic hydrocarbons in water-soluble fractions of Cook Inlet crude oil during an 18-day static exposure (1–21 day treatment) of walleye pollock eggs. Concentrations are means of three replicates measured by gas chromatography.

	0 days		4 days		18 days	
Hydrocarbon	ppm	%	ppm	%	ppm	%
benzene	1.424	51.0	0.808	50.6	0.057	26.4
toluene	0.845	30.3	0.432	27.0	0.000	0.0
ethylbenzene	0.007	0.2	0.000	0.0	0.000	0.0
m- and p-xylene	0.125	4.5	0.060	3.7	0.000	0.0
o-xylene	0.077	2.8	0.041	2.6	0.000	0.0
mesitylene	0.004	0.1	0.000	0.0	0.000	0.0
naphthalene	0.292	10.5	0.243	15.2	0.153	70.8
2-methylnapthalene	0.000	0.0	0.000	0.0	0.000	0.0
1-methylnapthalene	0.008	0.3	0.007	0.4	0.000	0.0
2,6-dimethylnapthalene	0.000	0.0	0.000	0.0	0.000	0.0
1,4-dimethylnapthalene	0.004	0.1	0.003	0.2	0.002	0.9
1,2-dimethylnapthalene	0.006	0.2	0.004	0.3	0.004	1.9
Total mononuclear aromatics	2.482	88.9	1.341	83.9	0.057	26.4
Total dinuclear aromatics	0.310	11.1	0.257	16.1	0.159	73.6
Total mono- and dinuclear aromatics	2.792	100.0	1.598	100.0	0.216	100.0
Percent total hydrocarbons remaining		100.0		57.2		7.7

Median lethal concentrations (LC_{50}) and median concentrations causing abnormalities (AB_{50}) were calculated with logit analysis (Berkson 1957) or Spearman-Karber analysis (Hamilton et al. 1977), corrected by control response (Abbott 1925).

Results

Test conditions

Monoaromatic hydrocarbons were initially predominant in the static WSF tests (89%), but they declined significantly more rapidly than diaromatic hydrocarbons ($P \ll 0.001$) (Table 3). After 18 days monoaromatics comprised only 26% of the remaining hydrocarbons (Table 3). The rate of total aromatic hydrocarbon loss from solution was not linear; rates were rapid initially, but slowed over time. Approximately one-half of the hydrocarbons were lost in the first 10 days. Concentrations reported in this paper are based on initial values.

Lethal effects

Egg survival and hatching success were slightly reduced (up to 17%) by exposure to WSF (Table 4). Reduction in survival and hatching success was significant in the 1–21 day treatment, but not in the 0–21 day and 7–21 day treatments. Mortality after hatch was strongly dependent on concentration (Fig. 1) and began to differ significantly from controls 29 days after fertilization, or about 10 days after hatch. The LC_{50} was 2.2 ± 0.8 ppm 10 days after hatch and stabilized at 1.8 ± 0.6 ppm 16 days after hatch.

Growth

Exposure to WSF before blastopore closure slowed early embryonic development. Blastopores in control embryos closed earlier than in embryos exposed to WSF (≥ 1.65 ppm) in the 0–21 day treatment (Table 5). Embryos in the 1-21 day treatment tended to have larger diameters at high WSF concentrations, but diameters were highly variable (Table 6). Pore diameters at 2.7 ppm were significantly greater than control diameters, but were significantly smaller at the lowest concentration (0.4 ppm). After blastopore closure, embryonic development in the upper concentrations could not be distinguished from control development, and the time of hatch was not influenced by exposure to WSF (Fig. 2).

Yolk and body lengths of larvae that hatched from eggs in the 0–21 day and 7–21 day treatments were significantly reduced by exposure to WSF ($P \leq 0.03$ [untransformed ANOVA]). (Lengths were not measured in the 1–21 day treatment.) Yolk lengths were reduced a maximum of 9%, total body lengths were reduced a maximum of 23% (Fig. 3), and the yolk-to-length ratio increased a maximum of 20%. Mean yolk lengths at concentrations ≥ 2.8 ppm were significantly ($P < 0.05$) smaller than controls. Reductions in larval body length in both treatments overlapped closely

Table 4

Walleye pollock egg survival and hatching success for treatment groups exposed to water-soluble fractions of Cook Inlet crude oil. ANOVA indicates significance of survival and hatching by analysis of variance; arc sine transformations were used with proportional data. NS $P>005$, $^{**}P \leq 0.01$, $^{***}P \leq 0.005$, † significant differences from control (Dunnette test, 95% confidence), and ±95% confidence interval.

0–21 day treatment				1–21 day treatment				7–21 day treatment			
ppm	*n*	% survival	% hatch	ppm	*n*	% survival	% hatch	ppm	*n*	% survival	% hatch
0.00	3	95.3 ± 5.0	88.0 ± 5.3	0.00	3	98.1 ± 5.2	97.1 ± 6.9	0.00	3	100.0 ± 0.0	100.0 ± 0.0
0.19	3	93.9 ± 8.6	86.9 ± 15.8	0.41	3	97.9 ± 6.4	96.8 ± 11.1	0.26	3	99.2 ± 3.5	99.2 ± 3.5
0.57	3	95.3 ± 8.3	87.4 ± 2.3	0.82	3	95.5 ± 6.9	95.5 ± 6.9	0.68	3	98.6 ± 3.7	98.6 ± 3.7
1.65	3	95.5 ± 5.0	84.9 ± 7.8	1.53	3	92.1 ± 2.5	89.7 ± 2.8	1.83	3	98.7 ± 3.0	98.7 ± 3.0
2.30	3	95.0 ± 8.3	87.6 ± 11.7	2.17	3	85.7 ± 11.3†	85.7 ± 11.2†	2.80	3	95.3 ± 1.3	95.3 ± 1.3
3.59	3	91.0 ± 4.1	84.3 ± 11.4	2.75	3	81.9 ± 17.0†	80.4 ± 18.4†	3.14	3	95.2 ± 16.1	95.2 ± 16.1
ANOVA		NS	NS			***	**			NS	NS

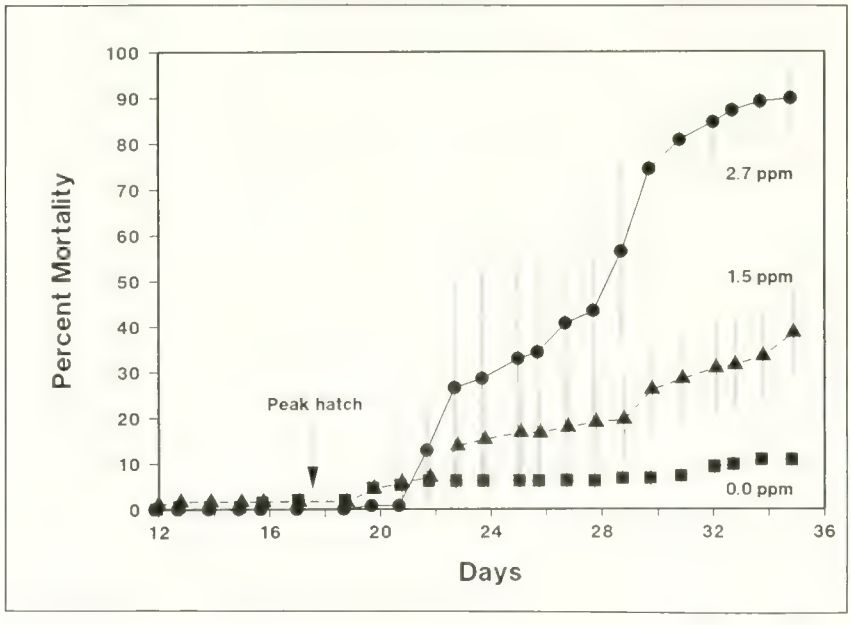

Figure 1
Percent mortality of walleye pollock larvae after hatch when embryos were exposed to water-soluble fractions of Cook Inlet crude oil (1–21 day treatment). Vertical bars are standard error.

Table 5

Blastopore closure in walleye pollock embryos 6 days after fertilization in the 0–21 day exposure to water-soluble fractions of Cook Inlet crude oil.

ppm	*n*	*n* closed	% closed
0.00	6	6	100.0
0.19	8	8	100.0
0.57	8	8	100.0
1.65	8	7	87.5
2.30	8	0	0.0
3.59	8	0	0.0

Table 6

Blastopore diameters of walleye pollock embryos 5 days after fertilization in the 1–21 day exposure to water-soluble fractions of Cook Inlet crude oil. ANOVA indicated significance of blastopore diameters by analysis of variance. $^{***}P \leq 0.005$, † significant differences from control (Dunnette test, 95% confidence), and ±95% confidence interval.

ppm	*n*	Diameter (mm)
0.00	30	0.13 ± 0.03
0.41	30	0.09 ± 0.02†
0.82	30	0.15 ± 0.02
1.53	30	0.15 ± 0.03
2.17	30	0.16 ± 0.02
2.75	30	0.19 ± 0.02†
ANOVA		***

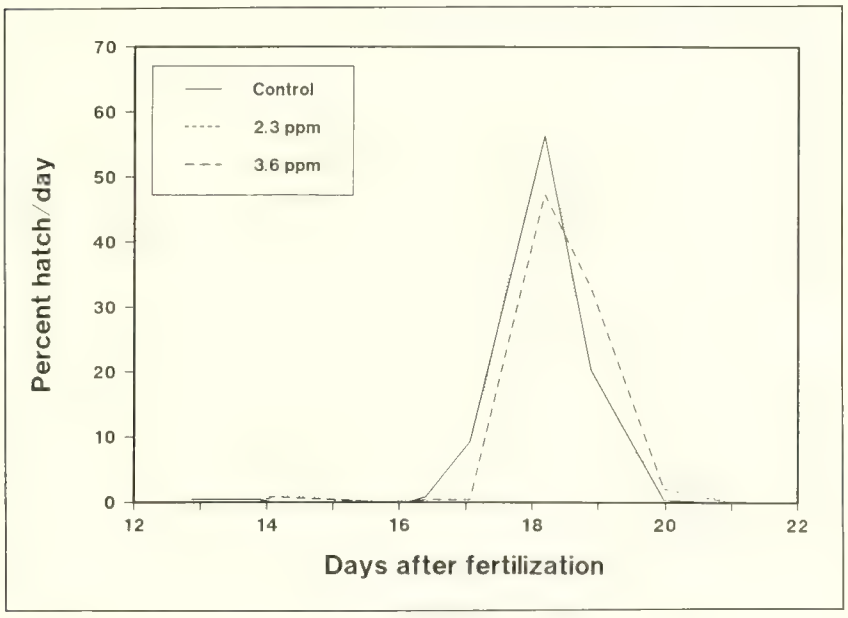

Figure 2
Timing of hatch (% per day) of walleye pollock when eggs were exposed to water-soluble fractions of Cook Inlet crude oil in the 0–21 day treatment.

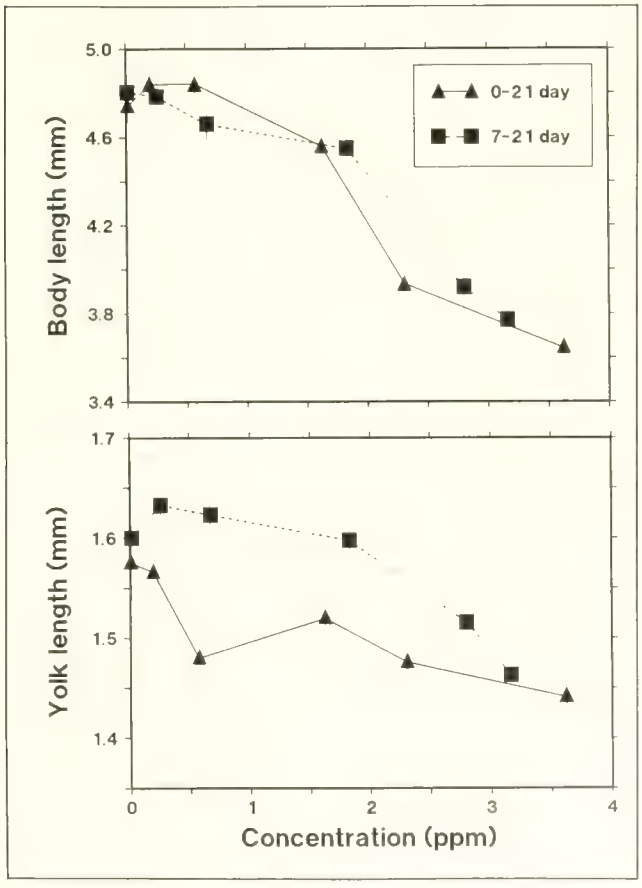

Figure 3
Length of yolks (measured along the major body axis) and total larval body lengths of walleye pollock plotted against concentrations of water-soluble fraction of Cook Inlet oil to which eggs were exposed. Vertical bars indicate 95% confidence interval.

(Fig. 3). Mean body lengths at concentrations ≥ 2.3 ppm were significantly ($P<0.05$) smaller than controls.

Abnormalities

Embryos exposed to WSF developed abnormalities. The earliest detected abnormality was the formation of membranous vesicles about the time of blastopore closure (days 6–9). In the 0–21 day treatment, embryos developed 1–5 vesicles along the ventral surface, usually posterior near the blastopore (Fig. 4). These vesicles were roughly spherical, apparently formed by a single membrane. Interior fluid was indistinguishable from surrounding fluid by observation of living specimens with a microscope. Frequency of occurrence and quantity of vesicles were correlated with concentration ($r=0.82$ and $r=0.67$, respectively), and vesicle size tended to increase with concentration (Table 7). The median concentration causing vesicle abnormalities was 2.4 ± 0.4 ppm. Vesicle formation was not observed in the 1–21 day or 7–21 day treatments; embryos in the 7–21 day treatment were beyond blastopore closure when exposure began.

Yolksac abnormalities were observed in exposed eggs shortly before hatch and other abnormalities occurred at and after hatch (Table 8). These abnormalities included body curvatures; deformations of yolk, eye, brain, jaw, intestine, and pericardial sac; absence of lower jaw; fin erosion; yolksac bloating; and light pigmentation. Yolksac bloating caused inverted floating. Correlation of abnormalities with concentration was strong ($r=0.9$ [logit transformation]). Correlation between abnormalities at hatch and vesicle

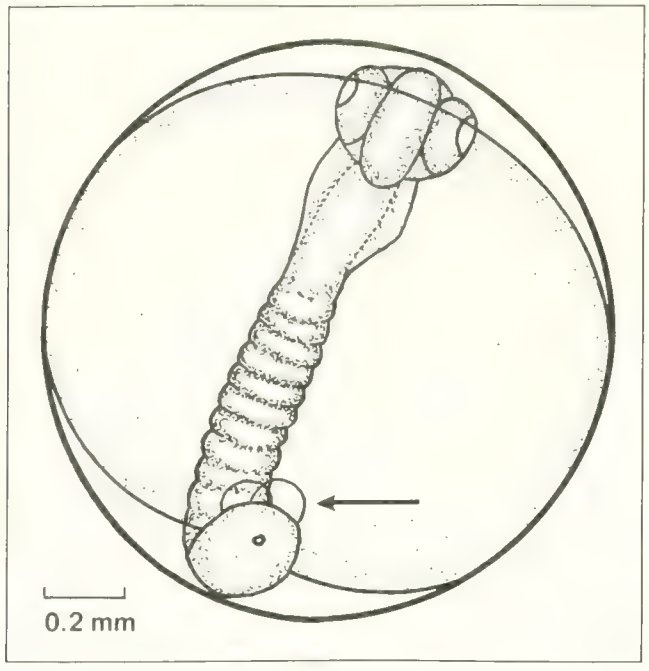

Figure 4

Walleye pollock embryos exposed to water-soluble fraction (3.6 ppm in the embryo shown) of Cook Inlet crude oil developed abnormal vesicles (arrow) along the ventral surface, usually posterior near the blastopore.

abnormalities was also high ($r = 0.99$). Median concentrations causing abnormalities at hatch ranged from 1.6 ± 0.2 to 2.1 ± 0.6 ppm (Table 8).

Deformed larvae did not recover from their abnormalities in clean water. In many cases the abnormalities became more pronounced as developing structures failed to form properly: 21 days after hatch a few abnormal larvae were still alive, but most (88%) had died (control mortality was 10%).

Discussion

Early embryonic development, as indicated by differences in blastopore diameters, was delayed by exposure to WSF, but the timing of hatch was not affected. Developmental stages (Yusa 1954) of controls and treated embryos were similar at all times except during blastopore closure. In other studies involving WSF tests of crude oils (Venezuelan, Iranian, Libyan), development of cod *Gadus morhua* embryos slowed, depending on concentration (Kühnhold 1974).

Genetic differences or differences in WSF preparations may account for the greater sensitivity observed in 1983 than in 1982. The WSF contained a higher proportion of diaromatic compounds in 1983 than in 1982, and diaromatics are generally more toxic than monoaromatics (Rice et al. 1977). However, these sensitivity differences were only in magnitude of response; basic response patterns were the same.

Increased metabolic demand may explain the observed reductions in yolk sizes of newly hatched larvae exposed to WSF during embryonic development. Yolk size was negatively correlated with concentration in both treatments, and yolk sizes tended to be smaller in embryos exposed for the longest period of time (0–21 day treatment), suggesting increased consumption of yolk and elevated metabolism. Linden (1978) also concluded that shorter lengths of larval Baltic herring *Clupea harengus membras* at hatching probably resulted from increased energy demands during exposure to the WSF of several oils. Other researchers have measured increases in metabolic rate directly; for

Table 7

Occurrence of vesicle abnormalities in developing walleye pollock embryos near time of blastopore closure in the 0–21 day exposure to water-soluble fraction of Cook Inlet crude oil. ANOVA indicates significance of abnormalities by analysis of variance; arc sine transformations were used with proportional data (% occurrence) or a square root transformation to control heterogeneity in the no./embryo test; $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.005$, † significant differences from control (Dunnette test, 95% confidence). Size codes: vs = very small, s = small, m = med.um, and l = large Large vesicles were 8.2% of the egg diameter (~0.11 mm).

	occurrence			*n*/embryo			
ppm	*n*	*X*	SE	Range	*X*	SE	Relative size
0.00	14	0	(0)	0–0	0.0	(0.0)	—
0.19	17	0	(0)	0–0	0.0	(0.0)	—
0.57	16	0	(0)	0–0	0.0	(0.0)	—
1.65	16	18	(6)	0–1	0.2	(0.1)	vs–m
[illegible]	16	25	(25)†	0–2	1.1	(0.2)†	s–l
3.59	14	78	(11)†	0–5	1.7	(0.4)†	m–l
ANOVA		**			***		
Regression		$r = 0.82$ *			$r = 0.67$ **		

Table 8

Percentage of walleye pollock larvae abnormal at the time of hatch following treatment in water-soluble fractions of Cook Inlet crude oil. ANOVA indicates significance of abnormalities by analysis of variance; arc sine transformations were used with proportional data. ***$P \leq 0.005$, † significant differences from control (Dunnette test, 95% confidence), and ±95% confidence.

0–21 day treatment			1–21 day treatment			7–21 day treatment		
ppm	*n*	% abnormal	ppm	*n*	% abnormal	ppm	*n*	% abnormal
0.00	3	2.4 ± 3.7	0.00	3	1.0 ± 4.2	0.00	3	6.4 ± 5.1
0.19	3	5.3 ± 9.5	0.41	3	1.0 ± 2.3	0.26	3	8.6 ± 13.4
0.57	3	5.4 ± 6.0	0.82	3	2.3 ± 7.0	0.68	3	6.6 ± 23.2
1.65	3	10.6 ± 13.6	1.53	3	51.2 ± 2.7†	1.83	3	16.4 ± 10.7
2.30	3	86.4 ± 5.5†	2.16	3	73.6 ± 15.4†	2.80	3	91.8 ± 12.4†
3.59	3	99.5 ± 2.2†	2.75	3	90.3 ± 11.5†	3.14	3	90.9 ± 9.2†
ANOVA		***			***			***

example, metabolic rates were elevated when larval Pacific herring *Clupea harengus pallasi* and northern anchovy *Engraulis mordax* were exposed to benzene (Struhsaker et al. 1974).

Decreases in larval size and yolk reserves caused by sublethal exposure of developing fish eggs to WSF potentially reduces survival potential. Predator avoidance capability tends to increase exponentially with larval length; however, decreases in avoidance behavior may be important only when the difference in size between predator and prey is small (Hunter 1981). Larvae with smaller yolk reserves generally have less time to begin feeding before onset of irreversible starvation (Blaxter and Hempel 1963).

The abnormalities observed in this study are the same, or similar, to those observed in other studies with a variety of species (Rosenthal and Alderdice 1976; Linden 1976; Kühnhold 1974, 1977) and support the observation by Rosenthal and Alderdice (1976) that fish embryos tend to respond developmentally in similar ways to external stress. Some of the developmental abnormalities (vesicle formation, body curvatures, and bloated yolks) caused by exposure of pollock eggs to WSF in this experiment were also caused by elevated temperatures in a pollock egg study by K. Krieger and L. Sonenberg (Auke Bay Lab., Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, P.O. Box 210155, Auke Bay, AK 99821, pers. commun. May 1988). Cold temperatures may cause similar problems in herring larvae: abnormal optic vesicles, enlarged pericardial areas, and jaw abnormalities (Ojaveer 1981). Lighter pigmentation in exposed cod *Gadus morhua* embryos has been observed in studies involving hydroxylated aromatic hydrocarbons (Falk-Petersen et al. 1985).

Ion imbalance due to changes in membrane osmoregulation (Ernst and Neff 1977, Linden 1978) provides a good explanation for yolksac and pericardial deformities, because yolksac volumes are related to water content (Rosenthal and Alderdice 1976). Aromatic hydrocarbons alter the surface properties of cell membranes, possibly modifying their permeability (Roubal and Collier 1975, Aronovich et al. 1975). Structural changes in cell and mitochondrial membranes of larval mummichogs *Fundulus heteroclitus* exposed to the WSF of Prudhoe Bay crude oil occurred even in larvae which did not show visible abnormalities (Cameron and Smith 1980).

Previous cell damage, rather than the continued presence of sequestered hydrocarbons, is most likely responsible for the development of abnormalities after hatch, because newly hatched larvae were transferred to clean water and most of the hydrocarbon depurated rapidly (59–83% in the first 8 hours; Carls and Rice 1988). In another study, cod larvae also depurated naphthalene quickly, but heavier organic compounds (phenanthrene, benzo(a)pyrene, and 2,4,5,2′,4′,5′-hexachlorobiphenyl) were depurated progressively more slowly as molecular weights increased (Solbakken et al. 1984). In our study, however, compounds with molecular weights greater than the methylnaphthalenes were present only at extremely low concentrations, if at all. An indication that the damage happened early in development, but was expressed later as malformations, was the occurrence of abnormal membranous vesicles 6–9 days after fertilization. At hatch, other malformations were observed which could have been the result of the same or similar mechanisms responsible for vesicle formation, and correlation between early and later abnormalities was very high ($r = 0.99$).

The significant mortality of larvae exposed to WSF during egg development was probably caused by biochemical changes, structural malformations, or disruption of tissue and organ development rather than a continued presence of hydrocarbons or insufficient yolk reserves. Larval mortality did not exceed 2%

until 3 days after the majority (89%) of the hatch was complete, ample time for most sequestered hydrocarbons to be depurated (Carls and Rice 1988). Some abnormal larvae (12% at 2.7 ppm) survived on their yolksac energy reserves to the end of the experiment (21 days after hatch), suggesting that depletion of endogenous energy was not responsible for mortalities occurring soon after hatch.

Oil accidently spilled in the marine environment rarely reaches concentrations (0.4–2.3 ppm) necessary to cause the effects observed in this study. However, the probability of oil spills is greater in nearshore waters, and this oil tends to concentrate in surface layers where walleye pollock eggs occur. For example, in the Bering Sea pollock eggs are spawned at depth and rise to the pelagic zone (Incze et al. 1984). Pollock eggs were most abundant in the upper 5–10 m, but abundance of older eggs (stage IV–VI) peaked about 20 m (Nishiyama et al. 1986, Serobaba 1974).

Large, single-event, nearshore oil spills have released sufficient quantities of hydrocarbons to affect planktonic fish eggs. For example, after the *Amoco Cadiz* spill, water entering the Aber Wrac'h estuary contained more than 1 ppm hydrocarbons and 0.5 ppm throughout the estuary (Calder and Boehm 1981). After the *Argo Merchant* grounded on Nantucket Shoals, about one-half the chorions of cod *Gadus morhua* and pollock *Pollachius virens* eggs were contaminated with oil droplets or tar, and approximately 20–46% of the eggs were dead or moribund, compared with a 4% control mortality (laboratory-spawned cod) (Longwell 1977).

In conclusion, exposure of pelagic marine walleye pollock eggs to WSF during development can cause embryos to develop abnormalities, and reduces size. Although they generally survive and hatch, embryos exposed to WSF produce abnormal larvae that have poor survival potential.

Acknowledgments

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Abstract.—The megalopal stage of *Cancer oregonensis* Dana is described from both laboratory-reared and naturally occurring populations in the Puget Sound Basin. It is compared with megalopae from natural populations of *C. productus* Randall collected in the same locale. Because megalopal characters of *C. productus* from these northern populations were found to differ significantly from those described by Trask (1970) for a California population, a redescription of the megalopa of *C. productus* based on the present collections is included. A key to the local megalopae of *Cancer* species, based on gross morphology, is presented.

A Comparative Study of the Megalopal Stages of *Cancer oregonensis* Dana and *C. productus* Randall (Decapoda: Brachyura: Cancridae) from the Northeastern Pacific

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The brachyuran crab genus *Cancer* Linnaeus is recognized throughout the world because of the major contributions of some of its species to commercial fisheries. Of the 13 Recent species reported in the Eastern Pacific (Nations 1975), four species, *C. gracilis* Dana, *C. magister* Dana, *C. oregonensis* Dana, and *C. productus* Randall, coexist in the Puget Sound Basin of Washington and British Columbia (Orensanz and Gallucci 1988). A fifth species, *C. branneri* Rathbun, has also been reported from the region (e.g., Rathbun 1904 [as *C. gibbosulus* DeHaan], 1930; Schmitt 1921 [as *C. gibbosulus*]; Kozloff 1974, 1987; Hart 1982). However, the only verified occurrences of *C. branneri* have been those cited by Rathbun (1904) for a single male from Port Althorp, Alaska (Natl. Mus. Nat. Hist., USNM 12516), and a second single male from Ucluelet, west coast of Vancouver Island, B.C. (USNM 40078). A specimen from Vancouver Island identified as *C. branneri* (Calif. Acad. Sci., CAS 015782) has proved to be *C. oregonensis* (personal examination). All subsequent records of *C. branneri* from the northeastern Pacific, north of the Oregon coast, are merely range listings based upon this early Rathbun material.

Of the four species indigenous to Puget Sound, *Cancer magister* (Dungeness crab) is the most thoroughly studied because of its commercial significance. However, catch records throughout its range exhibit considerable interannual fluctuations (Botsford 1986). Because of these fluctuations, fishery biologists have begun to examine the life history and larval dynamics of *C. magister* (e.g., Lough 1976, Reilly 1983). These studies suggested that larval and postlarval

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stages may hold the clue to periodic changes in the strength of year-classes. *Cancer* species pass through five larval (zoeal) and one postlarval (megalopal) stage. The megalopal stage represents the transition between the planktonic zoeae and the benthic adult. As the zoeae provide a major food source for several fish species (Garth and Abbott 1980), it is probable that the assessment of abundance of megalopae will provide the most reliable information on annual recruitment for commercial species. Therefore, it is essential that megalopae of the four species can be distinguished in mixed plankton tows. Information on the megalopal development of *C. magister*, *C. productus*, and *C. gracilis* are available; this is the first description of the megalopae of *C. oregonensis*.

Iwata and Konishi (1981) suggested that the setal formulae for the antenna and the endopod of the third maxilliped would permit specific identifications of the megalopae of several *Cancer* species, including *C. magister* and *C. productus*; however, their evaluation was made only from the published data available. Quintana and Saelzer (1986), in their summary of megalopal characters of *Cancer* species, remarked that endopodal setation of the third maxilliped was variable among species and very difficult to determine. They instead placed emphasis upon the setation of the epipod of the second maxilliped. Unfortunately, there often are considerable discrepancies between published descriptions of the same species. For example, Anderson (1978) emphasized the significance of the antennal setation in distinguishing megalopae of *C. anthonyi* Rathbun from *C. productus*. However, his setal count for *C. anthonyi* differed appreciably from that illustrated, but not specified, by Trask (1974) in his description of this species.

At least some morphological variation in larval characters may be attributed to differing geographic areas (Wencker et al. 1983, Shirley et al. 1987). We initially compared megalopae of *C. oregonensis* with megalopae of *C. productus* collected from Puget Sound. However, when we then compared the local *C. productus* megalopae with the description of megalopae from California (Trask 1970), we found substantive differences. Therefore, we have compared laboratory-reared and locally captured population of *C. oregonensis* megalopae with northern populations of *C. productus* megalopae and have redescribed the latter. From these descriptions, together with the descriptions provided by Poole (1966) for the megalopae of *C. magister* and Ally (1975) for *C. gracilis* magalopae, we have prepared a key to the megalopae of the northern populations of the four *Cancer* species.

Materials and methods

Samples from naturally occurring populations of megalopae of *Cancer oregonensis* and *C. productus* were collected from two broad regions within the Puget Sound Basin. The first region included 16 sites in the Strait of Georgia, British Columbia; the second consisted of 17 sites in the Strait of Juan de Fuca, Washington. Supplemental samples were also collected near Anacortes, Washington. Monthly sampling took place over a period of 5 months, May through September, 1987. Each sampling cruise consisted of nightly trawling with an otter neuston sampler (Mason and Phillips 1986) over a 3-day period. Megalopae were transferred to the laboratory and isolated in compartmented trays and maintained in a constant temperature unit (CTU) at 15°C in filtered seawater of 31‰. The megalopae were changed daily into fresh seawater, and newly-hatched *Artemia salina* (Linnaeus) nauplii were provided as nourishment. Exuviae were preserved in 70% ethyl alcohol. First crab instars were used to confirm species identifications. Twelve exuviae of each species were stained using 1% chorazol black in equal parts phenol and lactic acid; mouthparts and appendages were dissected and mounted in polyvinyl alcohol lactophenol. Morphological characters were then described and illustrations were made with the aid of a camera lucida mounted on a Wild M-5 stereomicroscope. An additional 42 exuviae of *C. oregonensis* and 48 exuviae of *C. productus* were examined for significant morphological characters not requiring dissection. Laboratory-reared megalopae of *C. oregonensis* were obtained from rearing studies. Six of the laboratory-reared megalopae were stained and dissected following the above procedure and an additional ten specimens were examined for gross morphology. Setal counts for all appendages are cited from proximal to distal.

Results

The megalopal stage of *Cancer oregonensis* is described from specimens collected from naturally occurring populations, and its morphological characters are compared with those of laboratory-reared individuals. Megalopae of *C. productus* from naturally occurring populations were similarly examined, and their morphological characters are compared with those described by Trask (1970) for a California population of this species (Table 1). Because a number of significant character differerences exist between the populations, a redescription of *C. productus* megalopae, based on the northern populations, is included.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Abbreviations used in the text are defined as follows: TL: Total length, measured from the tip of the rostrum to the midpoint of the telson; CL: Carapace length, measured from the tip of the rostrum to the posterior midpoint of the carapace.

Description: *Cancer oregonensis* Dana

TL 5.6–6.2 mm, CL 2.5–3.8 mm.

Carapace (Fig. 2A) Considerably longer than broad, lacking setae; lateral knobs usually absent, but with pair of gastric protuberances. Rostrum well developed. Dorsal spine projecting posteriorly over first two abdominal somites. Rostral region broad, with ventromedial tubercle. Eyes well developed, corneae slightly dilated.

Antennule (Fig 1A) Biramous; peduncle 3-segmented, proximal segment broadly expanded and with 6–14 scattered setae, penultimate segment with 4 or 5 submarginal setae distally, ultimate segment with 2 or 3 setae. Exopod 4-segmented, basal segment naked, 2nd segment with 7–13 aesthetascs, 3rd with 6–9 aesthetascs and 2 or 3 submarginal setae, 4th with 3–5 aesthetascs, 1 distomarginal seta and 1 terminal seta. Endopod indistinctly 2-segmented, proximal segment naked, distal segment with 2 or 3 marginal and 3 or 4 terminal setae.

Antenna (Fig. 1B) Peduncle 3-segmented, flagellum with 8 articles; setal formula varying from 3,2,4,0,0, 3,0,3,0,4,3 to 6,3,5,0,1,4,0,5,1,4,4.

Mandible (Fig. 1C) Molar and incisor processes not distinguishable. Mandibular palp 2-segmented, proximal segment naked, distal segment with 9–11 marginal setae.

Maxillule (Figure 1D) Endopod indistinctly 2-segmented, proximal segment with or without 1 marginal seta basally, distal segment with 1 or 2 terminal setae. Coxal endite with 13–16 setae. Basal endite with 23–29 total setae/spines including 4 or 5 distinct marginal setae basally.

Maxilla (Fig. 1E) Endopod broad basally, with 4–6 naked setae on outer margin in proximal half. Coxal endite with 3–6 terminal and 1–3 subterminal plumose setae on proximal lobe, 2–5 terminal and 1–3 subterminal plumose setae on distal lobe. Basal endite with 8–10 terminal and 1 or 2 subterminal plumose setae on proximal lobe and 8–11 terminal and 1 or 2 subterminal plumose setae on distal lobe. Scaphognathite with 68–85 marginal and 4 or 5 scattered surface setae (not shown in illustration).

First maxilliped (Fig. 1F) Epipod with 14–17 marginal or submarginal setae. Exopod 2-segmented, proximal segment with 2–4 plumose marginal setae distally, distal segment with 3–6 terminal plumose setae. Endopod 1-segmented with 1–3 marginal setae basally, 3–5 setae distally and 1 short terminal seta. Coxal endite with 15–20 setae. Basal endite with 26–35 setae.

Second maxilliped (Fig. 1G) Epipod with 6–9 marginal setae; protopod with 1–5 setae. Exopod 2-segmented, proximal segment with 1 or 2 short marginal spine-like setae, distal segment with 3–5 terminal plumose setae. Endopod 4-segmented, merus with 1–4 submarginal setae distally, carpus unarmed or with 1 or 2 marginal setae distally, propodus with 6–9 setae distally, dactyl with 8–11 marginal and submarginal setae, some distinctly serrate.

Third maxilliped (Fig. 1H) Epipod with 17–21 marginal setae; protopod with numerous scattered setae on surface. Exopod 2-segmented, proximal segment with 3–5 submarginal setae, distal segment with 4–8 terminal plumose setae. Endopod 5-segmented, ischium with inner margin somewhat denticulate, 24–32 marginal and/or submarginal and surface setae, merus with 9–13 setae, carpus with 14–19 setae, propodus with 12–18 simple and serrate setae, dactyl with 7-9 simple or serrate setae and 1 or 2 distinctly toothed bristles.

Pereopods (Figs. 2B,C,E–G) Segments of all pereopods with scattered short setae. Cheliped with ventral surface of ischium unarmed; cutting edge of fixed finger with 3 or 4 teeth, cutting edge of dactyl with 2–4 teeth. Second pereopod with coxa and ischium each armed with acute process on ventrodistal margin (Fig. 2D), latter 1/3 size of former; dactyl with 6 or 7 spines on ventral margin. Third, 4th and 5th pereopods lacking coxal and ischial processes. Dactyls with 4–8, 5–7 and 3 or 4 spines on ventral margins respectively; dactyl of 5th also with 3 terminal setae.

Abdomen and pleopods (Figs. 2A, 2H,I) Abdomen 6-segmented, segments unarmed. Second through 5th pleopods with 3–5, 4 or 5, 3 or 4, and 4 hooks respectively on appendix internae. Exopods with 20–22, 19–22, 17–22, and 17–19 plumose setae respectively. Uropods 2-segmented, peduncle with 1 marginal plumose seta, exopod with 11–13 plumose setae, endopod absent.

Telson (Fig. 2J) Dorsal surface with 3 or 4 pairs of short setae in midline distally, terminal margin slightly rounded, without marginal setae.

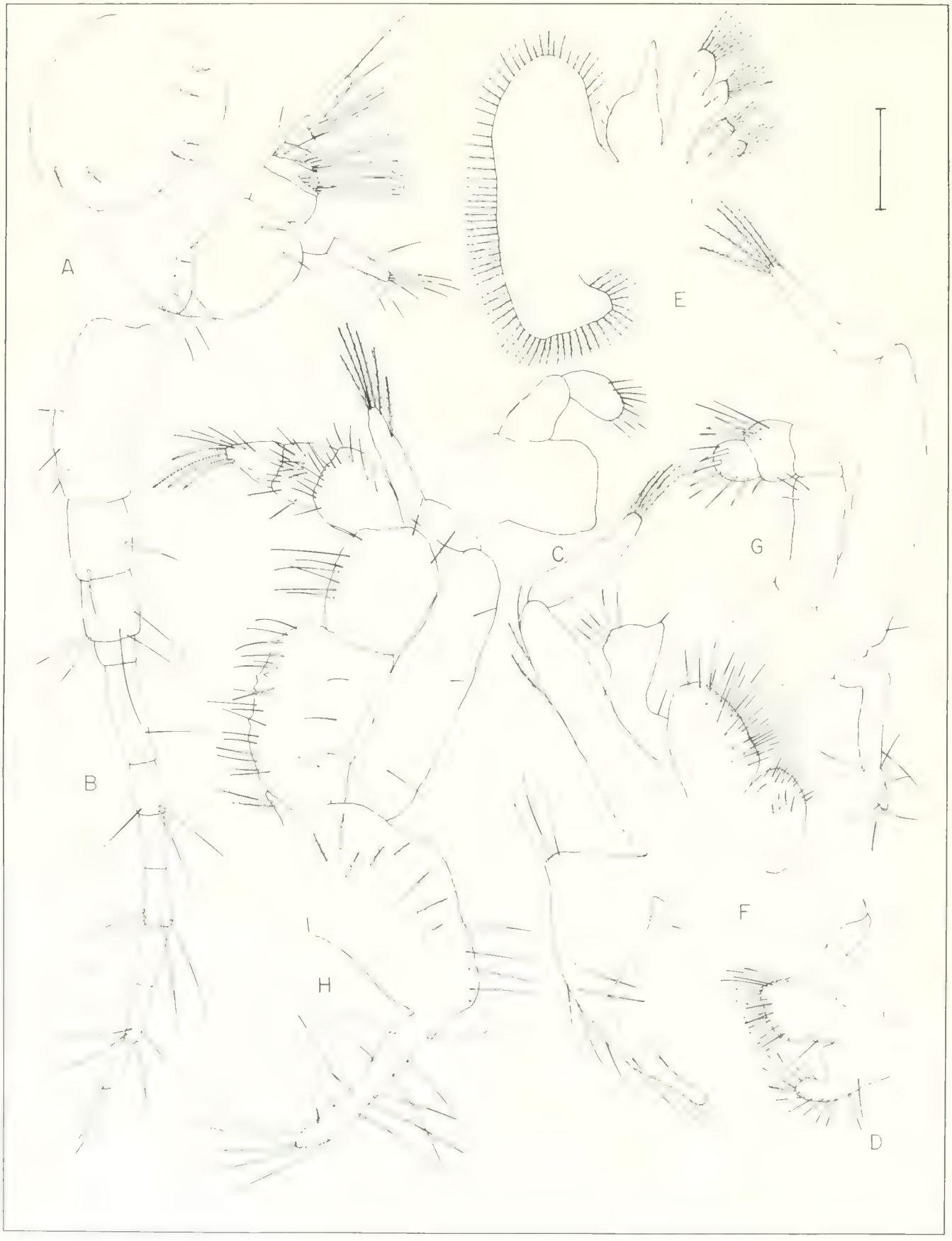
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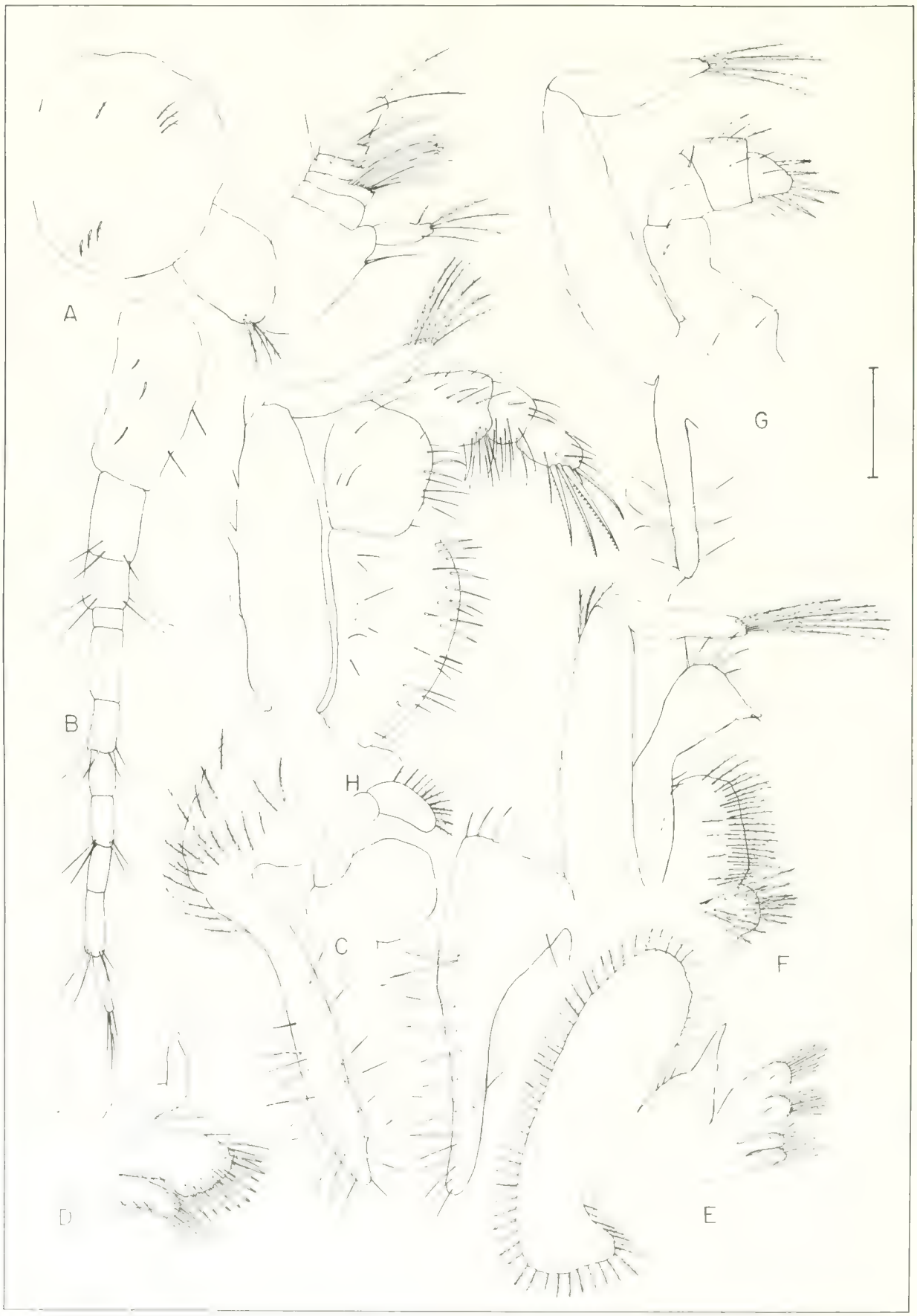
Figure 1

Megalopa of *Cancer oregonensis* Dana from Puget Sound Basin. (A) antennule; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla; (F) 1st maxilliped; (G) 2nd maxilliped; (H) 3rd maxilliped. Scale 0.1 mm.

Figure 2

Megalopa of *Cancer oregonensis* Dana from Puget Sound Basin. (A) whole animal (dorsal view); (B) cheliped; (C) 2nd pereopod; (D) coxae and bases (ventral view); (E) 3rd pereopod; (F) 4th pereopod; (G) 5th pereopod; (H) 2nd pleopod; (I) 5th pleopod; (J) telson and uropods. Scales 1.0 mm (A), 0.5 mm (B–G), and 0.1 mm (H–J).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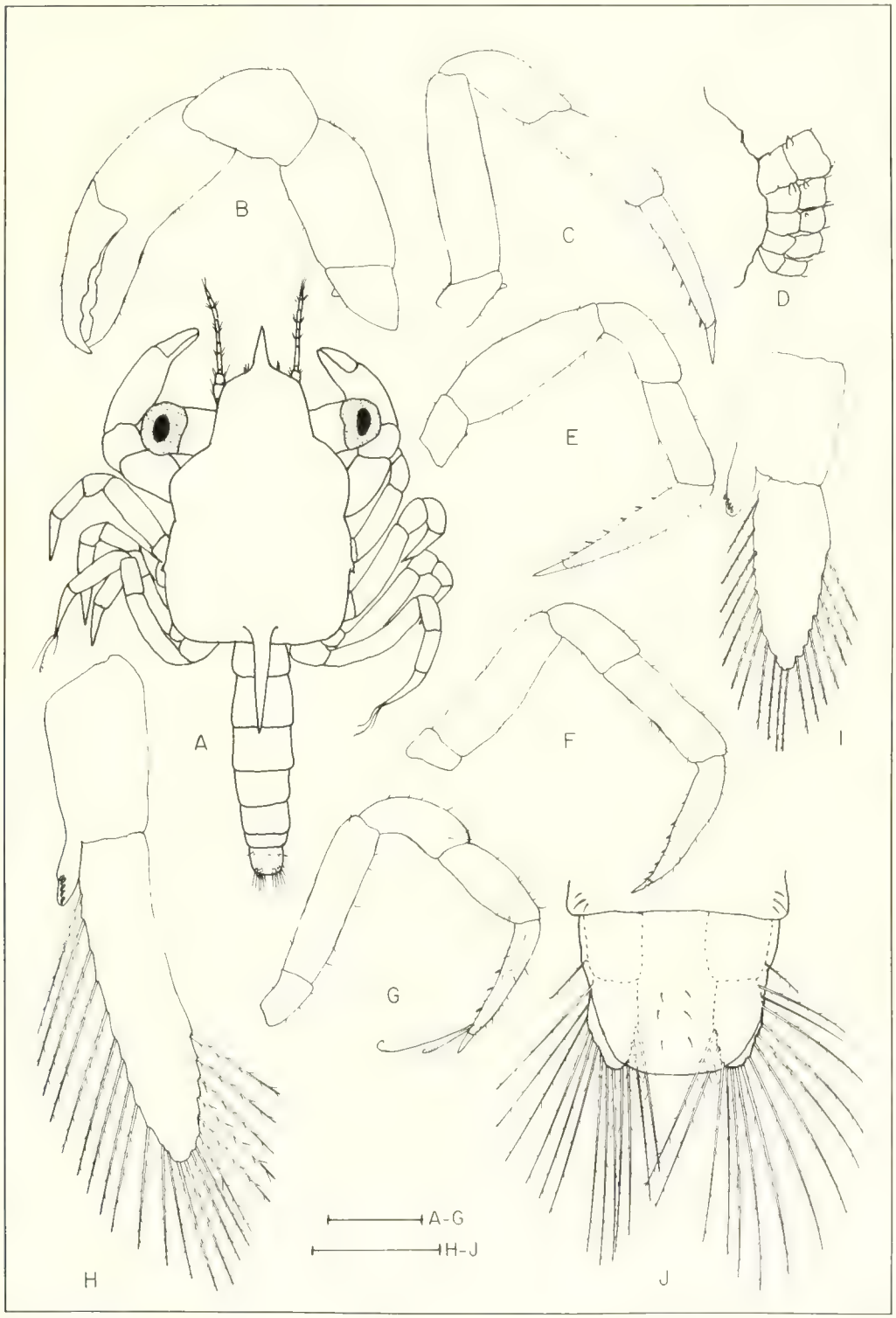

Figure 4
Megalopa of *Cancer productus* Randall for Puget Sound Basin. (A) whole animal (dorsal view; (B) chelped; (C) 2nd pereopod; (D) coxae and bases (ventral view); (E) 3rd pereopod; (F) 4th pereopod; (G) 5th pereopod; (H) 2nd pleopod; (I) 5th pleopod; (J) telson and uropods. Scales 1.0 mm (A), 0.5 mm (B–G), and 0.1 mm (H–J).

Figure 3
Megalopa of *Cancer productus* Randall from Puget Sound Basin. (A) antennule; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla; (F) 1st maxilliped; (G) 2nd maxilliped; (H) 3rd maxilliped. Scale 0.1 mm.

Table 1
Differences between Puget Sound Basin and California populations of *Cancer productus*.

	Puget Sound Basin (Present study)	California (Trask 1979)
Setal formulae		
Antenna		
peduncle plus flagellum	3,2,4,0,0,4,0,4,0,3,4 to 6,3,5,0,0,5,0,5,0,4,5	5,4,4,0,0,3,2,3,1,3,5
Maxilla		
scaphognathite	62–72	62–64
First maxilliped		
basal endite	28–38	38–40
coxal endite	15–19	9
Third maxilliped		
epipodite	20–29	13
exopod	5 or 6 + 5–9	–/+6
endopod		
segment 1	25–30	26*
segment 2	11–14	10*
segment 3	12–17	19*
segment 4	12–16	12*
segment 5	9–12	23*
Pleopodal exopod		
2nd	20–22	21
3rd	21 or 22	19
4th	20–23	19
5th	18–22	19
Armature		
Cheliped	Ischial process	
2nd pereopod	Coxal, ischial processes	–

—Not reported.
* Derived from figure.

Redescription: *Cancer productus* Randall

TL 5.6–6.4 mm, CL 3.1–3.6 mm.

Carapace (Fig. 4A) Considerably longer than broad, naked, lateral spines reduced to small, sometimes indistinct knobs, pair of gastric prominences present. Rostrum well developed and with ventromedial tubercle, dorsal spine projecting posteriorly over 1st and 2nd abdominal somites. Eyes well developed, corneae slightly dilated.

Antennule (Fig. 3A) Biramous; peduncle 3-segmented, proximal segment broadly expanded and with 6–14 scattered setae, penultumate segment with 3–5 distal plumose setae, ultimate segment with 1 seta. Exopod 4-segmented, basal segment naked, 2nd segment with 7–12 aesthetascs, 3rd segment with 5–9 aesthetascs and 2 or 3 marginal setae, 4th segment with 3–5 aesthetascs, 1 submarginal and 1 terminal seta. Endopod indistinctly 2-segmented, proximal segment naked, distal segment with 2 marginal and 3 or 4 terminal plumose setae.

Antenna (Fig. 3B) Peduncle 3-segmented; flagellum with 8 articles; setal formula varying from 4,2,4,0,0, 4,0,4,0,3,4 to 6,3,4,0,0,5,0,5,0,4,5.

Mandible (Fig. 3C) Molar and incisor processes not distinguishable. Mandibular palp 2-segmented, proximal segment naked, distal segment with 10–12 marginal setae.

Maxillule (Fig. 3D) Endopod indistinctly 2-segmented, proximal segment with 1 or 2 marginal setae, distal segment with 0–2 terminal setae. Coxal endite with 10–19 setae. Basal endite with 22–24 terminal setae/spines and 4 or 5 marginal setae basally.

Maxilla (Fig. 3E) Endopod expanded basally and with 4 marginal setae in proximal half, 1 short terminal seta. Proximal lobe of coxal endite with 2–4 terminal and 1 or 2 subterminal plumose setae, distal lobe with 2–5 terminal and 2 or 3 subterminal plumose setae. Proximal lobe of basal endite with 9 or 10 terminal and 1–3 subterminal plumose setae, distal lobe with 8 or 9 terminal and 1 subterminal plumose setae. Scaphognathite

with 62–72 marginal setae and 3–5 scattered surface setae (not shown in illustration).

First maxilliped (Fig. 3F) Epipod with 12–20 marginal and/or submarginal setae. Exopod 2-segmented, proximal segment with 3 or 4 marginal plumose setae distally, distal segment with 4–6 terminal plumose setae. Endopod with 1–3 marginal setae basally and 4–7 distally, 1 terminal seta; coxal endite with 15–19 plumose setae; basal endite with 28–38 plumose setae.

Second maxilliped (Fig. 3G) Epipod with 6–10 marginal setae; protopod with 1–7 scattered setae. Exopod 2-segmented, proximal segment with 1 or 2 marginal, short spine-like setae, distal segment with 4 or 5 terminal plumose setae. Endopod 4-segmented, merus with 2–6 setae, carpus with 2 or 3 setae, propodus with 5–9 setae, dactyl with 3–5 submarginal setae and 4–6 terminal serrate setae.

Third maxilliped (Fig. 3H) Epipod with 20–29 marginal setae. Protopod with 21–32 scattered plumose setae. Exopod 2-segmented, proximal segment with 5 or 6 marginal setae, distal segment with 5–9 terminal plumose setae. Endopod 5-segmented, ischium with 25–30 setae, merus with 11–14 setae, carpus with 12–17 setae, propodus with 12–16 setae, dactyl with 9–12 setae and 0–2 distinctly toothed bristles.

Pereopods (Figs. 4B,C, E–G) Segments of all pereopods with scattered short setae. Cheliped with ischium armed with acute spine on ventrodistal margin, cutting edge of fixed finger and dactyl each with 2–4 teeth. Second pereopod with coxa and ischium each armed with acute spine on distoventral margin (4D), ischial spine smaller than coxal spine, dactyl with 5–7 spines on ventral margin. Third pereopod with ischium frequently armed with minute process on ventrodistal margin, dactyl with 6 or 7 spines on ventral margin. Fourth and 5th pereopods with coxae and ischia unarmed, dactyls with 5–7 and 2–4 spines on ventral margin respectively; dactyl of fifth also with 3 terminal setae.

Abdomen and pleopods (Figs. 3A, 4H,I) Abdomen six-segmented. Second pleopod with 3–5 and 3rd through 5th each with 3 or 4 hooks on appendix internae. Exopods with 20–22, 21 or 22, 20–23, 18–22 plumose setae respectively. Uropods 2-segmented, peduncle naked or with 1 basal marginal plumose seta. Exopod with 12–13 plumose setae, endopod absent.

Telson (Fig. 4J) Dorsal surface with 3 or 4 pairs of short setae in midline distally, terminal margin usually slightly rounded, without marginal setae.

Discussion

Of concern to field biologists is the fact that larval studies primarily report characters found in specimens reared under laboratory conditions. Even though environmental conditions have been varied to ascertain their influence on larval development, there often remains a question as to the similarities of characters reported for these laboratory-reared organisms and those that would be found in naturally occurring populations of the same species. Although the megalopal characters of *Cancer oregonensis* and *C. productus* reported in this study were based upon specimens collected from naturally occurring populations, counts for some characters of *C. oregonensis* have been compared with counts derived from laboratory-reared animals. No appreciable differences were found between the two populations; however, in carapace length, the laboratory-reared individuals fell in the lower half of the length-frequency curve determined for the natural population.

As previously indicated, a number of differences between the megalopae of *C. productus* examined in this study and those described by Trask (1970) have been observed. Most obvious are the differences in setal formulae for the coxal endite of the first maxilliped and the epipod of the third maxilliped. Differences in antennal setation were also observed; however, Trask did not give a range for the number of setae occurring on each article, thus overlap between *C. oregonensis* and *C. productus* remains a possibility. Trask described the endopod of the 3rd maxilliped as four-segmented; however, five segments are clearly illustrated (1970, Fig. 7i). Quintana and Saelzer (1986) suggested that if the apparently contradictory descriptions of the megalopal stage of *Cancer anthonyi* Rathbun presented by Trask (1974) and Anderson (1978) were based on correct identifications and observations, geographical differences probably accounted for the great differences in the setation reported. A similar situation may account for the differences in *C. productus* megalopae.

Although Quintana and Saelzer (1986) recommend the use of the antennal setation, as well as the setation of the epipods of the maxillipeds, for distinguishing between *Cancer* megalopae, these characters cannot be used to separate Puget Sound populations with any degree of reliability. The antennal setation found in *C. oregonensis* overlaps that reported for *C. gracilis*; only the setae of the antepenultimate article differ between *C. oregonensis* and *C. productus*. The setation reported for *C. magister* that we have determined from the figure presented by Poole (1966, Fig. 6C) differs from counts made for northern specimens. With the exceptions of larger numbers of setae on the epipods

of the first and second maxillipeds of *C. magister*, setal numbers for the maxillipedal epipods overlap among all four local species.

In his description of the larval development of *Cancer magister*, Poole stated that the megalopa possessed five abdominal segments and a telson, and this number was repeated by both Ingle (1981) and Iwata and Konishi (1981) in their reviews of megalopal characters of *Cancer* species. As all other described larvae possess a six-segmented abdomen, this single character would be expected to provide a very simple and easy means for recognizing megalopae of *C. magister*. Poole's (1966) description of the megalopae was based on two specimens collected from Drakes Bay, California; however, Poole indicated that he had compared these individuals with laboratory-reared specimens. He noted no significant differences. His figure (1966: fig 6A) indicates no suture between the sixth abdominal somite and the telson, and he refers to the uropods as the "pleopods of the telson." Unless a major, and evolutionarily significant, variation occurs in the postlarvae of this species over its range, Poole's description is incorrect. We have examined a substantial number of *C. magister* megalopae from the Puget Sound Basin, and in all cases the sixth abdominal somite is clearly separated from the telson by a well marked suture; the uropods arise, as in other megalopae, from the distal margin of the sixth somite.

Megalopae of *Cancer* have been broadly grouped by Orensanz and Gallucci (1988) into the size categories small, medium, and large. In the species of local interest, *C. gracilis* is grouped among those species with small megalopae: *C. oregonensis* and *C. productus* in the medium-sized group and *C. magister* as the single representative in the large category. However, Orensanz and Gallucci have reported a bimodal recruitment of *C. magister*, with the late-summer megalopae being of considerably smaller size. Thus the use of size in distinguishing *C. magister* from other local species may be less reliable during certain periods of the year than previously assumed. The megalopae of *C. oregonensis* and *C. productus* are morphologically very close and no definitive means of distinguishing between the two species at this stage has been available. During the course of this study an apparently constant and easily recognizable character has been found that will distinguish *C. productus* from *C. oregonensis*, i.e., the presence in the former species of an acute process on the ventral surface of the ischium of the cheliped (Fig. 4D) that is absent in the latter species (Fig. 2D). In fact, the absence of a spine or process on the ischium of the cheliped distinguishes *C. oregonensis* megalopae from all three of the other local species. Poole (1966) described a spine only on the "basi-ischipoidite of the first walking leg" of *C. magister*; however, in our northern populations we have found that a strong, acute spine is present on the ventrodistal margin on the ischium of the cheliped and on the ventrodistal margin of the coxa of the 2nd and 3rd pereopods. Ally (1975) reports a spine ("hook") on the ventral surface of the ischium of the cheliped in *C. gracilis*. We have not been able to examine local megalopae of this species; therefore, in preparing the following key to the local species, we have relied on the completeness and accuracy of Ally's description.

Key to the megalopae of northern populations of *Cancer*

1 No spine or process on ventrodistal surface/margin of ischium of cheliped .... ***C. oregonensis***
Acute spine or process on ventrodistal surface/margin of ischium of cheliped 2
2 Megalopae of small size (<3.0 mm); 2nd and 3rd pereopods lacking coxal spine or process on ventrodistal surface ..... ***C. gracilis***
Megalopae of medium to large size (<4.0 mm); 2nd pereopod with coxal spine or process on ventrodistal surface.....3
3 Megalopae with acute spine on ventrodistal surface of coxa of 3rd pereopod..... ***C. magister***
Megalopae usually without process, or rarely with very small process on ventrodistal surface of coxa of 3rd pereopod ..... ***C. productus***

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Abstract.– Peak beach-seine catches of small (60–120 mm FL) juvenile fall chinook salmon in Coos Bay occurred about 30–45 days after peak seine catches farther upstream in the Coos and Millacoma Rivers. The average time between release and capture in the bay of marked hatchery fall chinook salmon was about 30 days, but ranged up to 83 days. Thus, many small hatchery and wild fall chinook salmon remained in Coos Bay for about 1 month before entering the ocean. Most captures of large (123–156 mm mean FL) tagged spring chinook salmon released directly into the bay occurred within 10 days following release, indicating a shorter period of residence in the bay for spring chinook salmon than for fall chinook salmon. Catches of juvenile spring chinook salmon were very patchy. Potential for competition between juvenile fall and spring chinook salmon in Coos Bay may be reduced because of differences in the timing and locations of maximum abundance of these two groups. Fin-clipped fall chinook salmon grew at least 0.2–0.5 mm per day.

Distribution and Residence Times of Juvenile Fall and Spring Chinook Salmon in Coos Bay, Oregon

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Estuaries are important rearing habitats for subyearling chinook salmon (Healey 1982, Reimers 1973, Myers 1980, Nicholas and Hankin 1988, Levy and Northcote 1982). Residence in estuaries of subyearling chinook salmon can be as long as 3 months or more (Reimers 1973, Myers 1980). Growth rates of subyearling chinook salmon are high in some estuaries (Healey 1980, Levings et al. 1986, Argue et al. 1986), but low in others, perhaps because of competition for food (Reimers 1973, Neilson et al. 1985). Because of the long period of residence and active feeding of juvenile chinook salmon in estuaries, the release of large numbers of hatchery chinook salmon into a system could impact survival and growth of wild fish. The interactions among groups of chinook salmon depend on their overlap in the estuary in time and space.

Many large subyearling spring chinook salmon smolts were released in 1987 into Coos Bay, Oregon, by Anadromous, Inc., a private salmon ranching facility. These fish ranged from about 120 to 160 mm mean fork length (FL) and were generally larger than wild subyearling chinook salmon found in Oregon estuaries (Reimers 1973, Myers 1980, Nicholas and Hankin 1988). The large spring chinook salmon may compete with smaller fall chinook salmon for estuarine resources. However, estuarine dependency and emigration rates of spring and fall chinook salmon in Coos Bay are not known. To assess the potential for competition between juvenile spring chinook salmon released by Anadromous, Inc. and fall chinook salmon, we studied their temporal and spatial overlap in beach-seine samples.

Methods

We collected juvenile chinook salmon in Coos Bay (lat. 43°21′N, long. 124°20′W) with a 60 × 2.5 m beach seine between 25 April and 10 October 1987. The seine had 19- and 13-mm mesh (stretch-measure) in the wings and bunt, respectively. The net was set with the current using a 6.1-m dory powered by a 50 hp outboard motor. Juvenile salmon were counted, measured, and checked for fin-clips immediately after capture. When catches were large, juvenile salmon were kept alive in a floating net pen during processing. Salinity was estimated with an American Optical (Model TS) refractometer to the nearest ‰ and temperature measured to the nearest 0.1°C.

Five stations were sampled regularly (Fig. 1). Stations 1, 2, 3, 4, and 5 were 2.0, 3.3, 6.5, 9.8, and 14.8 km, respectively, from the mouth of the bay. The Anadromous, Inc. release facility was located on North Spit between sites 3 and 4. On most dates each station was sampled twice.

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Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

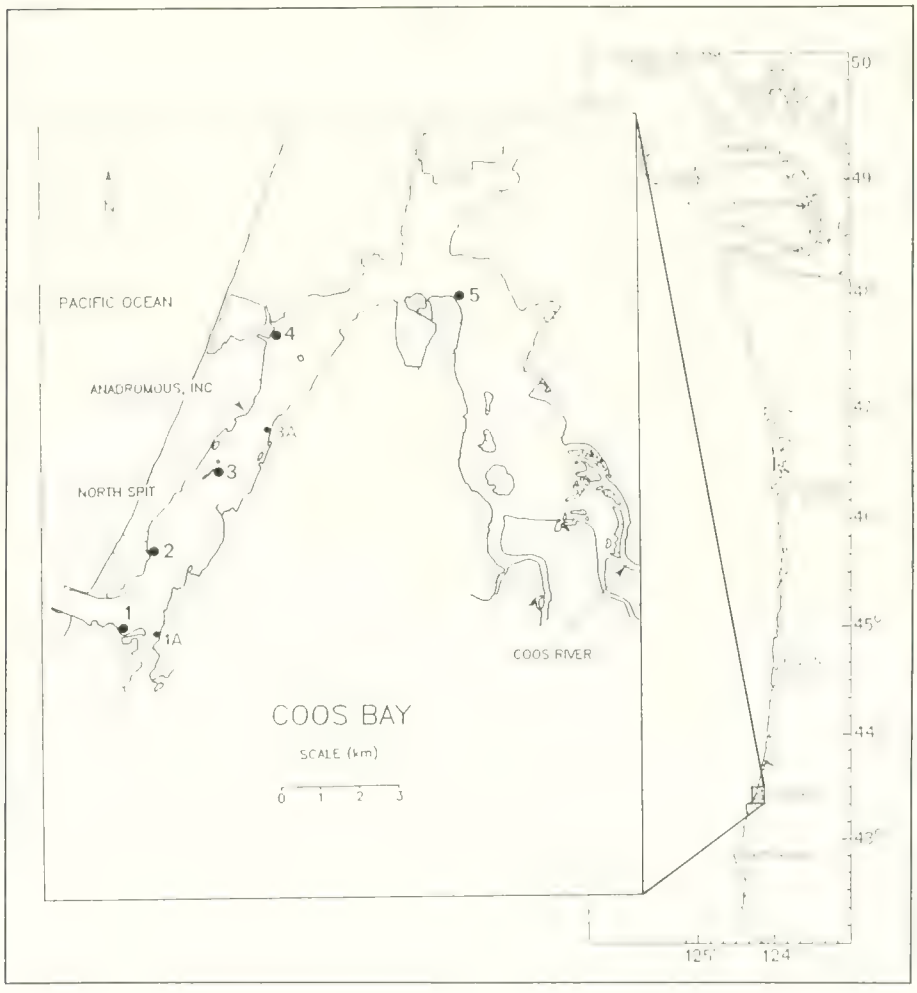

Figure 1

Coos Bay, Oregon, showing five stations routinely sampled and two sites occasionally sampled (1A and 3A) for juvenile chinook salmon with a beach seine in 1987. The Anadromous, Inc. release site on North Spit is indicated by an arrow. The Millacoma River (not shown) is a tributary of the Coos River. Also shown are other estuaries mentioned in the Discussion.

Generally, we sampled from the lower to the upper bay in the morning and in the opposite direction in the afternoon. Occasionally sets were made at two other sites (1A and 3A in Fig. 1).

The substrate at all stations was sand except at station 5 where it was gravel and mud. During low tide the seine usually sampled parts of eel grass beds at stations 2, 3, and 4.

About 415,000 subyearling fall chinook salmon were released in 1987 by the Salmon and Trout Enhancement Program (STEP) into tidewater tributaries of the Coos River between 27 and 35 km above station 5 (Fig. 1). These subyearling fall chinook salmon were released between 30 April and 28 June (half before and half after 23 May). Average fork length (FL) of fish at release ranged from approximately 48 to 94 mm (converted from mean weights, T. Rumreich and R. Bender, Oreg. Dep. Fish Wildl., P.O. Box 5430, Charleston, OR 97420, pers. commun., March 1988). Of STEP fall chinook salmon released in 1987, 74% were supposed to be fin-clipped. However, the actual percentage of fish with recognizable marks was not known because marking efficiency was not evaluated. Wild fall chinook salmon caught in the lower Millacoma and Coos Rivers were about the same size as STEP fish.

Over 5 million subyearling spring chinook salmon were released into Coos Bay in eight groups between 19 June and 1 October 1987 from Anadromous, Inc.'s holding and release facility located on North Spit (Fig. 1). These spring chinook salmon were considerably larger than the STEP or wild fall chinook salmon and averaged 123–156 mm FL at release. Between 0 and 5.9% (average 3.6%) of the fish in each group were coded-wire tagged (CWT) and had clipped adipose fins. We sampled the bay 1–2 days before and after each Anadromous, Inc. release and at about weekly intervals between releases.

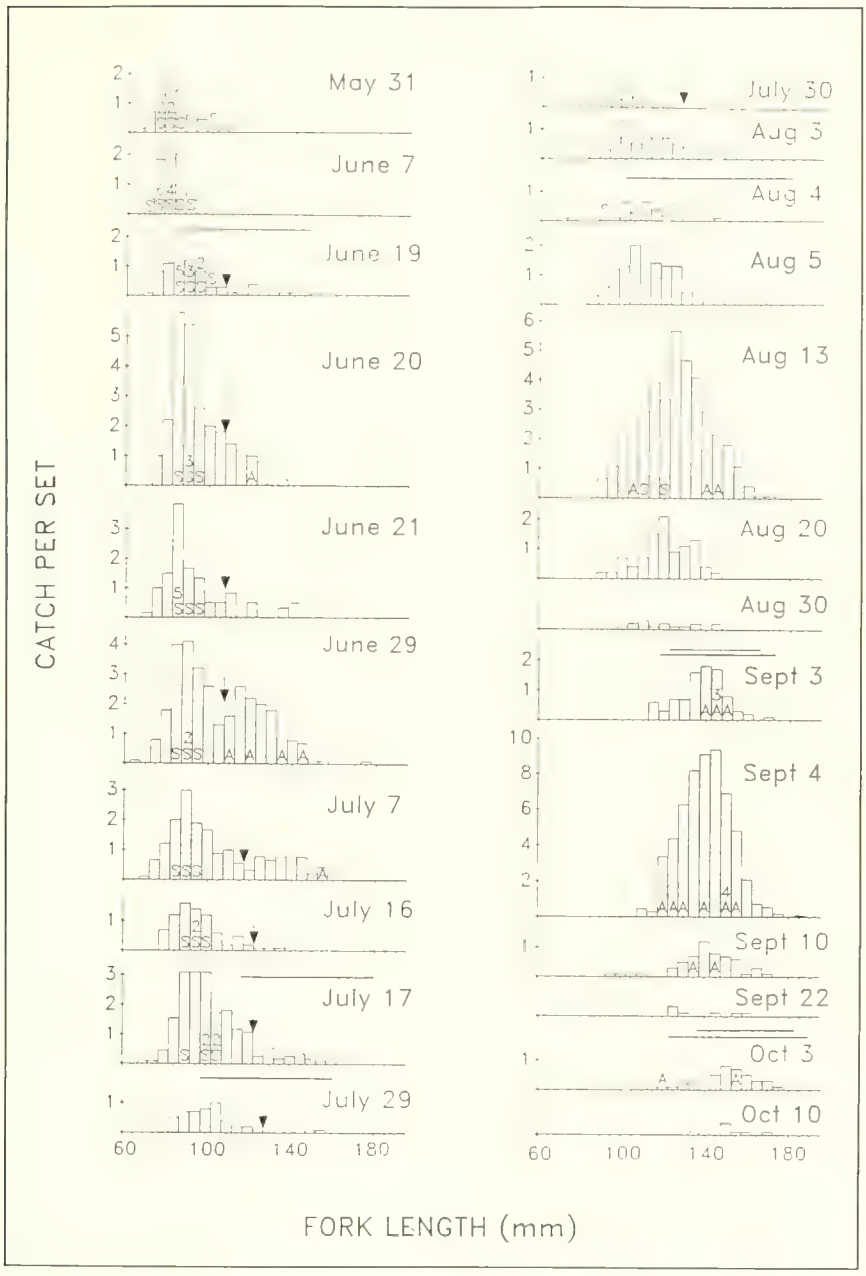

Figure 2
Length-frequency distributions of juvenile chinook salmon caught in Coos Bay, Oregon, in beach seines in 1987. Numbers of marked fall chinook salmon released by the Salmon and Trout Enhancement Program (S) and spring chinook salmon released from Anadromous, Inc. (A) caught in each length category are indicated. An "A" or "S" without a number represents a single fish. Heavy horizontal lines indicate lengths (±2 SD) of production groups of spring chinook salmon released by Anadromous, Inc. Arrows indicate the lengths used to separate fall and spring chinook.

Results

Immigration of fall chinook salmon

Juvenile wild and STEP fall chinook salmon were caught in the bay in large numbers starting in late May (Fig. 2). Only two juvenile chinook salmon were captured during our first two sampling trips on 25–26 April (8 sets) and 9 May (6 sets). Catches of juvenile wild and STEP fish in the lower reaches of the Millacoma and Coos Rivers entering the bay peaked on 15 May and 26 May, respectively, and declined to low levels after mid-June (R. Bender, Oreg. Dep. Fish Wildl., P.O. Box 5430, Charleston, OR 97420, pers. commun., March 1988).

Size-frequency distributions

Distinct modes in the length-frequency distribution of juvenile chinook salmon provided a basis for separating small STEP and wild fall chinook salmon from large Anadromous, Inc. chinook salmon until the end of July (Fig. 2). Recoveries of fin-clipped STEP fall chinook salmon (S in Figure 2) confirmed that the mode of small

fish was mainly fall chinook salmon from 31 May through the end of July. Almost all fall chinook salmon captured before the first release of spring chinook salmon on 19 June were less than 105 mm FL. Although we caught some large spring chinook salmon after the first release on 19 June, a large, distinct mode of these fish was not apparent until 10 days later on 29 June. Recoveries of Anadromous, Inc. spring chinook salmon with CWTs (A in Figure 2) indicated that this second mode of large fish was mostly spring chinook salmon. This mode of large-sized fish was also obvious a week later on 7 July, but by 16 and 17 July catches of large fish had decreased to low levels. Catches of large chinook salmon did not increase immediately following the 17 and 29 July releases.

We classified fish as either fall or spring chinook salmon to estimate their relative abundances in the bay. On 19, 20, and 21 June fish that were ≤105 mm FL were considered fall chinook salmon and the larger fish were considered spring chinook salmon. (Arrows in Figure 2 indicate the division between these groups). On 29 June and 7 July, we used the valley between the two distinct modes to separate fall and spring chinook salmon. To account for growth of fish, we distinguished fall and spring chinook salmon at slightly larger lengths on 16, 17 July and 29, 30 July (120 and 125 mm FL, respectively). In August, length ranges of fall and spring chinook salmon overlapped and the two groups could not be separated by length. However, catch per set of fall chinook salmon on 29 and 30 July was lower than it had been in June and earlier in July, suggesting that abundance of fall chinook salmon probably peaked in June and July. Catches of fin-clipped fall chinook salmon (S in Figure 2) in August were also low compared with earlier periods. Therefore, we assumed that subsequent increases in catch per set of juvenile chinook salmon in August (Fig. 2) were due almost exclusively to releases of large spring chinook salmon from Anadromous, Inc. In the following discussion we have treated all fish caught starting 3 August as spring chinook salmon, realizing that this probably overestimates the abundance of spring chinook salmon in the bay, especially in early August when a few marked fall chinook salmon were caught.

The proportions of adipose clipped or CWT fish in our catches of spring chinook salmon were usually similar to the proportions of CWT fish in the immediately preceding releases of spring chinook salmon from Anadromous, Inc. (χ^2 tests, $p>0.05$) (Table 1). This supports the conclusion that most fish we classified as spring chinook salmon originated from the Anadromous, Inc. facility. An exception was during the period 4–30 August when the proportion of CWT fish in our catch of spring chinook salmon was significantly lower than the proportion released by Anadromous, Inc. on 4 August ($\chi^2=6.14$, $p<0.025$). This result may be explained by lack of complete mixing of marked and unmarked Anadromous, Inc. fish and their patchy distribution. Over 77% of the catch in August occurred in just five sets, three of which were on the same day. Large numbers of fall chinook salmon in the bay in August mistakenly classified as spring chinook salmon also could have produced the low proportion of CWT fish. However, there is little direct evidence that fall chinook salmon were abundant in the bay during August since very few fin-clipped fish were recovered, although regeneration of fins may have made recognition of marks difficult (R. Bender, Oreg. Dep. Fish Wildl., P.O. Box 5430, Charleston, OR 97420, pers. commun., March 1988).

Table 1

Percentage of coded-wire tagged (CWT) or adipose clipped fish in the catch of spring chinook salmon from Coos Bay, Oregon, vs. the percentage of CWT fish in the preceding release from Anadromous, Inc.

	Catch		Anadromous, Inc.	
Period	n	% CWT[a]	% CWT in release	χ
6/19–7/7	232	2.6	2.3	0.08
7/17–8/3	92	1.1	2.5	0.75
8/4–8/30	751	0.7	1.9	6.14[b]
9/3–9/22	775	2.3	2.9	0.93
10/3–10/10	50	4.0	5.9	0.32

[a]Includes 16 Anadromous, Inc. CWT fish, 11 fish with unreadable CWTs probably from Anadromous Inc., and 5 adipose-clipped fish without tags.
[b]Observed frequency of tags is significantly different from expected frequency, $p<0.025$.

Catch distribution

Before mid-June, roughly equal numbers of fall chinook salmon were caught at each of the five standard stations (Fig. 3). After mid-June, fall chinook salmon were concentrated near the mouth of the bay at station 1, although they were also caught at the other stations. At station 1, catch per set of fall chinook salmon peaked in June and July and dropped to low levels at the end of July (Fig. 3).

Catches of Anadromous, Inc. spring chinook salmon were extremely patchy, with large catches at one or two stations and low catches at the others. After the first release on 19 June, almost all spring chinook salmon were found upbay at station 5, but later releases were caught at the lower bay stations 1, 1A (not shown), and 2 (Fig. 3). Catch per set of spring chinook

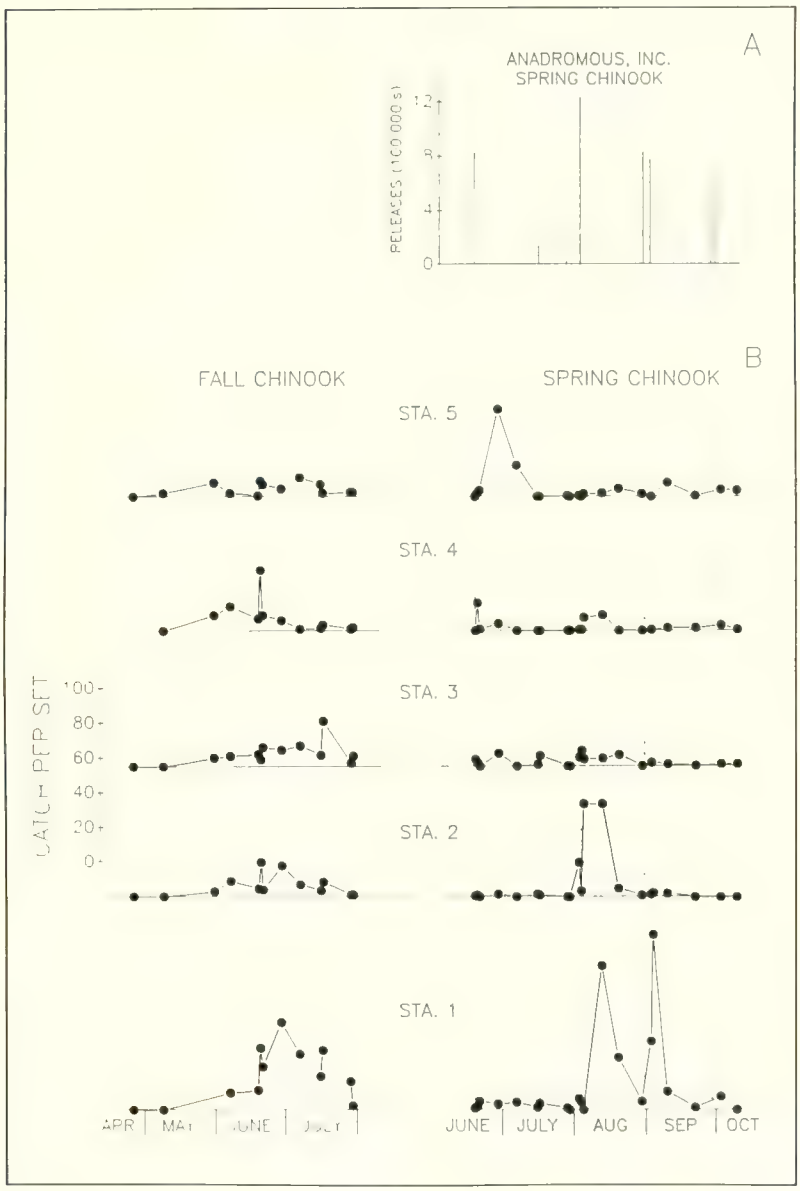

Figure 3

(A) Numbers of spring chinook salmon released in 1987 into Coos Bay, Oregon, by Anadromous, Inc. (B) Mean catch per set of fall and spring chinook salmon by station. Dotted lines indicate release dates.

salmon peaked 10 days, 1–9 days and 1–4 days following the 19 June, 4 August, and 31 August–3 September releases, respectively, and generally fell to low levels in the inter-release periods. Little increase in catch per set followed the 29 September and 1 October releases.

In general, the distribution in the bay of marked fall and spring chinook salmon was consistent with the distribution of unmarked fish. Mean catch per set of fin-clipped fall chinook salmon was much greater at lower bay stations 1 and 1A than at any other stations (Table 2). On average, all fin-clipped fish were caught at station 1 about 13 days later than at upbay stations 4 and 5 (Table 2), suggesting a gradual movement of fish downbay. However, among individual mark groups the trend for later capture in the lower bay than in the upper bay was clear only for right-pelvic clipped fish. Most (4 of 6) CWT fish from the 19 June release of spring chinook salmon were caught upbay at station 5, and none were caught downbay at stations 1 or 2. In contrast, after the 4 August release, one CWT fish was found at each of stations 1, 2, and 3, and, after the 31 August release, 15 of 16 CWT fish were recovered downbay at station 1.

Juvenile spring chinook salmon were found in large aggregations (67% of the total catch occurred in 5% of the sets) while STEP and wild fall chinook salmon were more evenly dispersed. Spring chinook salmon were present in only 60% of sets after the first release, whereas fall chinook salmon occurred in 95% of sets between 9 May and 30 July.

Table 2

Mean catch per set (CPUE) of fin-clipped fall chinook salmon and mean days between release and recovery at each site in Coos Bay, Oregon, for each of four mark groups.

Station	No. sets (5/9–8/13)	Fin-clipped fish recovered	Mean CPUE	Mean days between release and recovery*				
				RP_2	An	Dor	LP_2	All combined
Upbay								
5	29	8	0.27	1	38	35	18	19
4	28	6	0.21	21				21
3	28	3	0.11	23	30			29
3A	3	1	0.33	23				23
2	28	9	0.32	26	23			25
1	27	34	1.25	37	30	23	18	33
1A	1	2	2.00		83		46	65
Downbay								

*Mean days = Σ(CPUE(d) · d)/ΣCPUE(d), where CPUE(d) = number tags recovered/number of sets on day following release = d.
RP_2 = right pelvic, An = anal, Dor = dorsal, and LP_2 = left pelvic clip

No consistent relationship was found between water temperature and catch of juvenile chinook salmon. Temperatures measured on the bottom at about 0.3 m depth generally changed little between May and October but increased with distance from the mouth of the bay, averaging 12.3, 11.9, 13.8, 15.0, and 16.8°C at stations 1–5, respectively, for all sampling dates combined. The large catches of juvenile spring chinook salmon at stations 1 and 2 and of juvenile fall chinook salmon at station 1 (Fig. 3) occurred at water temperatures between 9–14°C. However, large catches of spring chinook salmon also occurred at station 5 in June and July at temperatures above 17°C. Surface salinity was high at all stations during the study period (usually >29‰ after mid-June), indicating little influence of freshwater at our sampling sites. (See also Burt and McAlister 1959.)

Residence in the bay

Unmarked STEP or wild fall chinook salmon resided in the shallow nearshore areas of the bay for about 1–2 months. Catch per set of fall chinook salmon was highest between 20 June and 17 July (Fig. 3), about 1.0–1.5 months later than the peak catches in the river systems just above the bay (R. Bender, Oreg. Dep. Fish Wildl., P.O. Box 5430, Charleston, OR 97420, pers. commun., March 1988).

Mean duration of residence in the bay of 63 fin-clipped STEP fall chinook salmon was about 1 month (Table 2). The average number of days (weighted by catch per set of the marked fish) between release of the median fish in a mark group and recovery in the bay of fish from that same mark group was 29 days (n = 63, range −6 to 83 days). Eight fin-clipped fish were caught more than 50 days after release. The number of days between release of the last fish in a mark-group and the recovery in the bay of fish from that same mark-group, a minimal estimate of time since release, averaged 24 days (n = 63, range −13 to 81 days). Average recovery date of right-pelvic and anal fin-clipped fish was 27 and 32 days, respectively, after release of the median fish (Table 2).

Peak catch per set of spring chinook salmon usually occurred within 1–10 days after Anadromous, Inc. releases, and catches declined rapidly afterwards, suggesting that spring chinook salmon had a much shorter period of residence in shallow waters of the bay than fall chinook salmon (Fig. 3). Catches returned to low levels within about 25 days following the releases on 19 June and 29 July–4 August and within 7–10 days following the releases on 31 August and 3 September. The very rapid decline in catch per set after the 31 August and 3 September releases, together with the low catches of fish from the last two releases on 29 September and 1 October, indicate that movement into deepwater channels or out of the bay for these late summer releases may have been more rapid than for earlier releases.

All but one of the 27 CWT Anadromous, Inc. spring chinook salmon caught in beach seines were captured 10 or fewer days after release* (range 1–18 days);

*Tags from eleven of these fish were unreadable; however, these unreadable tags were probably from the 31 Aug. and 1 Oct. releases (Mary McGowan, Anadromous, Inc., P.O. Box 1007, North Bend, OR 97459, pers. commun., Jan. 1989).

another indication that residence of spring chinook salmon in the bay is relatively short. Moreover, CWT spring chinook salmon from each release were recovered only during the period before the next release.

Growth rates

Growth rates of anal and right-pelvic clipped fall chinook salmon, estimated from the slopes of the linear regressions of fork length on days since release of the median fish, were 0.54 mm/day ($n = 19$, $r^2 = 0.74$) and 0.29 mm/day ($n = 33$, $r^2 = 0.33$), respectively. Because emigration from the bay may be positively related to fish size, these observed growth rates probably underestimate the true average rates of growth of fish in the mark groups.

Discussion

Our data indicate that small fall chinook salmon reside in Coos Bay for a longer period than do larger spring chinook salmon. Duration of residence in estuaries may be related to the size or stock of fish. Dawley et al. (1986) found that rates of downstream movement of subyearling chinook salmon from lower Columbia River stocks were positively related to fish length. Movement of small subyearling fish through the Columbia River estuary decreased by 30% relative to movement rates farther upstream, while larger yearling fish moved through the estuary at the same rate as through the river. Neither subyearling nor yearling fish, however, reared for long periods in the Columbia River estuary.

Because our collections were made by beach seine in shallow nearshore areas of Coos Bay, we can say little about the utilization of deeper channel areas by juvenile fall and spring chinook salmon. We do not know whether peak abundances of fall or spring chinook salmon in channels coincide with peak abundances in shallow areas. Neither do we know what fraction of fall or spring chinook salmon at any given time are in shallow or channel areas. Temporal and size-related differences in utilization of nearshore and channel areas by juvenile chinook salmon have been found in other estuaries and also may occur in Coos Bay. (See Figure 1 for locations of other estuaries discussed.) In Yaquina Bay, Myers (1980) found that although catches in shallow areas peaked in late July and early August, catches continued to increase in channels into October. In both Yaquina Bay and the Columbia River estuary, small fish and large fish preferentially utilized nearshore and channel areas, respectively. The mean lengths of wild juvenile chinook salmon in beach seine (nearshore) and lampara net (channel) catches in Yaquina Bay during June were 88 and 106 mm FL, respectively (Myers 1980). In the upper Columbia River estuary, many more yearling chinook salmon (large fish) were caught in channels than in nearshore areas and, conversely, more subyearling chinook salmon (smaller fish) were found in nearshore areas than in channels (Dawley et al. 1986). In addition, subyearling fall chinook salmon caught in nearshore areas were 10–20 mm shorter than those caught in channel areas, and catch rates of subyearling chinook salmon in nearshore areas were inversely related to length (Dawley et al. 1986). If similar size-related distributional patterns occur in Coos Bay, then the large spring chinook salmon released from Anadromous, Inc. may utilize channel areas much more extensively than shallow nearshore areas.

Delays of up to 10 days occurred between releases of spring chinook salmon from the Anadromous, Inc. facility and peak catches of juvenile spring chinook salmon in nearby (<8 km distant) shallow areas (Figs. 2 and 3). This suggests that spring chinook salmon may stay in channels for several days following release and then disperse into shallow waters. Some of the spring chinook salmon occurring at stations 1 and 2 near the mouth of the bay, especially those found several days after a release, may even have reentered the shallows from the ocean. Two CWT juvenile chinook salmon released earlier in 1987 in Yaquina Bay were found later in Coos Bay at station 1. This demonstrates that juvenile chinook salmon, after they have entered the ocean, sometimes reenter estuaries.

The apparent rates of growth in length for two groups of fin-clipped STEP fall chinook salmon caught in Coos Bay (0.29 and 0.54 mm/day) were similar to rates reported for a group of marked subyearling fish caught in the upper Columbia River estuary (Dawley et al. 1986; 0.60 mm/day) and reported by Levings et al. (1986) for fry caught in the Campbell River estuary (0.46–0.70 mm/day) but lower than reported by Healey (1980) for fry in Nanaimo Estuary (1.32 mm/day) or by Argue et al. (1986) for smolts in Cowichan Bay (0.97 mm/day). All these calculations of growth rates were based on changes in length of marked fish with time and should have a similar bias (i.e., possible faster emigration of fast-growing or large fish that results in underestimates of actual mean growth rates attained in the bay). Reimers (1973) reported little change in size of marked and unmarked fish in the Sixes estuary June through August, after which growth rates increased dramatically. He attributed the slow growth of juvenile fish during the June–August period to their high densities in the bay. Myers (1980) found substantial increases in size of wild chinook salmon with time and between the upper and lower bay, indicating substantial growth of wild chinook salmon. Thus growth of juvenile chinook salmon appears to vary among estuaries, perhaps depending on their density and food supply.

An interesting feature of the catch distribution of fall and spring chinook salmon in Coos Bay (Fig. 3) is that when the catch of fall chinook salmon was highest at the downbay station 1 (20 June–29 July), the catch of spring chinook salmon at this station was low. Conversely, when the catch of spring chinook salmon was high at the upbay station 5 (29 June–7 July), the catch of fall chinook salmon at this station was relatively low. Later in the summer when most spring chinook salmon were released, fewer fall chinook salmon were caught in the bay. Apparently peak abundances of juvenile fall and spring chinook salmon differed in time and place. The potential for competition between these two stocks was probably greatest in June and July after the large release of spring chinook salmon and when large numbers of fall chinook salmon were present in shallow nearshore areas of the bay. However, since the two groups were found at different sites, direct competition may have been limited.

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Abstract. – Three species of basses of the genus *Paralabrax* are found in southern California coastal waters. Adults can be identified on the basis of morphological characters, but the eggs and early larval stages of the three species are extremely similar in appearance. This paper reports an investigation of biochemical genetic characters for specific identification. An electrophoretic analysis of 43 presumptive gene loci demonstrated several genetic differences between any two of the three species, but no single locus was able to unambiguously distinguish the three species. In contrast, an analysis of *Paralabrax* mitochondrial DNA (mtDNA) demonstrated that 8 of 13 informative restriction endonuleases produced species-specific fragment patterns. A technique is described for the relatively rapid enrichment and analysis of mtDNA from both fresh and ethanol-preserved individual eggs and early larvae which allows specific identification on a cost-effective basis.

Biochemical Genetics of Southern California Basses of the Genus *Paralabrax*: Specific Identification of Fresh and Ethanol-preserved Individual Eggs and Early Larvae

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The serranid genus *Paralabrax* is endemic to the eastern Pacific Ocean and comprises seven species. Three species, the kelp bass *P. clathratus*, barred sand bass *P. nebulifer*, and spotted sand bass *P. maculatofasciatus*, are common in southern California coastal waters and all are important components of the California sport fishery (Oliphant 1979). Adults of these three species can be separated on the basis of morphological differences (Miller and Lea 1972); however, it is not possible at this time to determine the specific identity of field-caught *Parlabrax* eggs, larvae, or early juveniles using morphological characters (Butler et al. 1982; R. Lavenberg, Los Ang. Cty. Mus. Nat. Hist., Los Angeles, CA 90007, pers. commun., June 1988). Ecological studies of the early life history of the three species, as well as stock assessment studies based on the early-life-history stages, have been hampered by the inability to specifically identify *Paralabrax* eggs and larvae.

A variety of biochemical characters have been used to identify the eggs and larval forms of closely related fishes in the absence of discriminating morphological characters. Electrophoresis of water soluble proteins (allozyme analysis) has been used to differentiate species of marine fishes which have morphologically similar eggs, larvae and early juvenile stages (Morgan 1975, Smith and Crossland 1977, Sidell et al. 1978, Smith et al. 1980, Mork et al. 1983, Graves et al. 1989). However, due to the small sizes of eggs and larvae, and the possibility of low enzyme activity during early-life-history stages, some studies have reported difficulty in resolving the electrophoretic bands of eggs and very small larvae (Smith and Crossland 1977, Sidell et al. 1978, Smith et al. 1980, Graves et al. 1989).

Restriction endonuclease analysis of mitochondrial DNA (mtDNA) has

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been used to demonstrate intra- and interspecific genetic relationships among and within various marine and freshwater fishes (Ferris and Berg 1987). This technique provides an additional tool for the investigation of egg and larval identities. Although original protocols were costly, time-consuming, and generally not applicable to the small amount of tissue available with early-life-history forms, a modification of existing methodologies has provided a relatively simple method for distinguishing the eggs and larvae of closely related (congeneric) species. In this paper, we report the results of an investigation of water-soluble protein and mtDNA restriction fragment differentiation among the three southern California species of *Paralabrax* to find a reliable genetic marker to discriminate the early-life-history stages of the three species. A cost-effective means of analyzing mtDNA restriction fragments of both fresh and ethanol-preserved individual eggs is presented.

Materials and methods

Adult specimens of the three *Paralabrax* species were collected by hook and line, pole spear, and beach seine off San Diego and La Jolla, California. After collection, fish were transported to the laboratory alive or on ice. Samples of liver, eye, and muscle tissue were removed and frozen at −25°C until electrophoretic analysis was undertaken. Gonads and livers were removed and used fresh or stored at −70°C for mtDNA analysis.

Eggs and larvae of the three species were obtained from a captive brood stock maintained at the Southern California Edison research facility in Redondo Beach, California. Eggs were collected within 12 hours of spawning and either transported to the laboratory in San Diego in seawater or preserved in 95% ethanol.

Protein electrophoresis

Four specimens each of *Paralabrax maculatofasciatus* and *P. nebulifer* were collected for the electrophoretic investigation. The sample of *P. clathratus* (45) was larger because individuals were collected as part of a more extensive investigation of gene flow within southern California coastal fishes (Waples and Rosenblatt 1987). Samples of muscle, liver, and eye tissue were individually macerated in an approximately equal volume of 0.1 M potassium phosphate buffer, pH 7.0, before centrifugation for 10 minutes at 16,000 g, 5°C. Supernatants were loaded on horizontal starch gels using procedures similar to those described by Selander et al. (1971). Staining recipes for the 24 enzyme and protein systems studied (Table 1) were modified from Shaw and Prasad (1970) and Harris and Hopkinson (1976). A more detailed description of the electrophoretic procedures, including all staining recipes, is presented in Waples (1986).

Proteins encoded by multiple genes (isozymes) were numbered according to decreasing anodal mobility. For each gene locus the mobility of the most common allele in *Paralabrax clathratus* was arbitrarily designated 100, and alternate alleles were numbered in accordance with their mobility relative to this standard. Genetic similarity and genetic distance were computed from the allele frequency data using Nei's (1978) method, which corrects for small sample size.

Mitochondrial DNA analysis

Mitochondrial DNA for restriction analysis was purified from fresh or frozen gonad or liver samples from six individuals of each species following the protocols for equilibrium density gradient ultracentrifugation of Lansman et al. (1981), with minor modifications. Typical yields were 1 microgram of mtDNA per gram of fresh tissue.

A mini-prep procedure was developed for isolating mtDNA from small tissue samples based on the techniques described by Chapman and Powers (1984). Tissue samples as small as an individual egg (0.6 mg) were homogenized in 0.15 mL 10 mmol/L TRIS, 10 mmol/L EDTA, pH 7.4 (TE buffer) in a 0.2-mL ground glass homogenizer. The homogenate was transfered to a 1.5 mL microfuge tube and an additional 0.5 ml of TE buffer added. The tube was spun at 800 g, 4°C, for 3 minutes to remove nuclei and cellular debris. The supernatant was transferred to a second microfuge tube and centrifuged at 12,000 g, 4°C, for 20 minutes to pellet mitochondria. The mitochondrial pellet was resuspended in 0.4 mL TE buffer and lysed with 0.04 mL 10% SDS. The mitochondrial lysate was extracted with an equal volume of a 25:24:1 phenol/chloroform/isoamyl alcohol solution and then an equal volume of 24:1 chloroform/isoamyl alcohol. The DNA from the aqueous layer, after the addition of ammonium acetate, was precipitated in two volumes of 95% ethanol at −70°C for at least 2 hours.

The following restriction endonucleases employed in this study were purchased from Bethesda Research Laboratories (BRL) and used according to the supplier's instructions: *Aca*I, *Aca*II, *Bam*HI, *Bgl*II, *Bst*EII, *Cla*I, *Eco*RI, *Hinc*II, *Hind*III, *Hin*fI, *Hpa*II, *Kpn*I, *Pst*I, *Pvu*II, *Sal*I, *Sma*I, *Sst*I, *Xba*I, and *Xho*I. Endlabelling was performed according to the protocols of Brown (1980), with the exception that an ethanol precipitation was not necessary for digestions with restriction endonucleases that recognized six base pairs. Electrophoresis of restriction fragments was performed on both large and mini-submarine horizontal

Table 1

Enzymes and proteins surveyed and tissues and buffers used in the electrophoretic analysis of three species of *Paralabrax*.

Protein (EC number)	Locus	Buffer*	Tissue**
Aconitate hydratase (4.2.1.3)	Acon	1	l
Adenosine deaminase (3.5.4.4)	Ada	1	m
Adenylate kinase (2.7.4.3)	Ak	1	l
Alcohol dehydrogenase (1.1.1.1)	Adh-1	2	l
	Adh-2	2	l
Aspartate aminotransferase (2.6.1.1)	Aat-1,2	1,2	l
Creatine kinase (2.7.3.2)	Ck-A	2	m
	Ck-B	2	e
Esterase (3.1.1.–); α-naphthyl acetate	Est-1,2,3	3	m
Fumarte hydratase (4.2.1.2)	Fum	1	l
Glucose-6 phosphate dehydrogenase (1.1.1.49)	G6pdh	1	l
Glucosephosphate isomerase (5.3.1.9)	Gpi-A	2,3	m,l
	Gpi-B	2,3	m
Glutamate dehydrogenase (1.4.1.2)	Gdh	1	l
Glyceraldehyde-phosphate dehydrogenase (1.2.1.12)	Gapdh-1	1	l
	Gapdh-2	1	m
Glycerol-3-phosphate dehydrogenase (1.1.1.8)	G3pdh-A	1	m
	G3pdh-B	1	l
Iditol dehydrogenase (1.1.1.14)	Iddh	1	l
Isocitrate dehydrogenase (NADP) (1.1.1.42)	Icdh-s	1	m
	Icdh-m	1	l
Lactate dehydrogenase (1.1.1.27)	Ldh-A	1	m,e
	Ldh-B,C	1	e
Malate dehydrogenase (1.1.1.37)	Mdh-A,B,m	1	m
Mannosephosphate isomerase (5.3.1.8)	Mpi	1	l
Phosphoglucomutase (5.4.2.2)	Pgm	2	m
Phosphogluconate dehydrogenase (1.1.1.44)	Pgdh	1	m
Peptidase (3.4.11.–); leucyl-tyrosine	Pep-1	3	m
Peptidase (3.4.11.–); leucylglycyl-glycine	Pep-2	3	m
Peptidase (3.4.11.–); non-specific	Pep-3	3	m
Superoxide dismutase (1.15.1.1)	Sod	2	l
Xanthine dehydrogenase (1.1.1.204)	Xdh	1	l
General proteins	Pro-1,2,3,4,5	3	m

**Buffers: 1 = Tris-citric acid, pH 6.9 (Whitt 1970); 2 = Tris-citric acid, pH 8.0 (Selander et al. 1971); 3 = Lithium hydroxide (Selander et al. 1971).

**m = muscle, l = liver, e = eye.

agarose gels (0.8–1.2%) and vertical polyacrylamide gels (3.5–5.0%) at 3 volts/cm.

The Southern transfer and hybridization protocols of Maniatis et al. (1982) were followed. Hybridization probe mtDNA (purified *Paralabrax* mtDNA) was nick translated with biotinylated dATP using the procedures of the BRL Nick Translation System. Visualization of the fragments followed the procedures included with the BRL BluGene Gene Detection Kit.

The mean mtDNA nucleotide sequence divergence between the three *Paralabrax* species was calculated from the number of shared fragments using the algorithm of Nei and Tajima (1983).

Results

In the electrophoretic analysis, 43 presumptive gene loci could be resolved in all three species (Table 1). The genetic interpretation of observed banding patterns was guided by expectations based on known patterns of tissue specificity of expression and subunit composition of enzymes in fishes and other vertebrates. Discussion of banding patterns for each enzyme system can be found in Waples (1986). Twenty-two loci were monomorphic (fixed for the same allele) in all individuals

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 2
Allele frequencies at variable loci in three *Paralabrax* species.

Locus/Allele		*P. clathratus*	*P. nebulifer*	*P. maculatofasciatus*
Aat-1	130	-	-	0.167
	100	1.0	1.0	0.833
	2N	90	6	6
Ada	100	0.878	-	-
	90*	0.111	-	-
	82	0.011	0.167	1.0
	60	-	0.833	-
	2N	90	6	8
Adh-2	-100	1.0	-	0.833
	-300	-	1.0	-
	-500	-	-	0.167
	2N	70	4	6
Ck-2	120	-	1.0	1.0
(Ck-A)	100	1.0	-	-
	2N	62	8	2
Est-3	108	-	-	1.0
	100	0.988	1.0	-
	94	0.012	-	-
	2N	82	6	6
Gapdh-2	100	0.989	-	1.0
	-1200	0.011	1.0	-
	2N	90	8	6
G3pdh-2	100	1.0	0.125	1.0
(G3pdh-A)	60	-	0.875	-
	2N	90	8	8
Gpi-2	150	-	0.25	-
(Gpi-B)	100	1.0	0.75	1.0
	2N	90	8	8
G6pdh	100	1.0	-	1.0
	90	-	1.0	-
	2N	50	4	4
Icdh-1	100	1.0	-	-
(Icdh-s)	95	-	1.0	1.0
	2N	10	6	6
Icdh-2	100	1.0	0.875	0.875
(Icdh-m)	95	-	0.125	0.125
	2N	40	8	8
Iddh	100	1.0	1.0	0.75
	-500	-	-	0.25
	2N	10	4	4
Mpi	100	0.986	-	-
	95	0.014	1.0	1.0
	2N	70	4	4
Pgdh	124	-	1.0	1.0
	100	1.0	-	-
	2N	40	6	4
Pgm	100	0.989	0.25	-
	73	0.011	0.75	1.0
	2N	90	8	8
Pep-1	108	0.012	-	-
	100	0.988	1.0	1.0
	2N	82	8	8
Pep-2	110	-	0.125	-
	100	1.0	0.875	1.0
	2N	42	8	8
Pep-3	110	0.011	-	-
	100	0.989	1.0	1.0
	2N	90	8	8
Pro-2	110	-	-	1.0
	100	1.0	1.0	-
	2N	90	8	8
Pro-4	100	1.0	-	1.0
	80	-	1.0	-
	2N	78	6	6
Sod	105	-	1.0	1.0
	100	1.0	-	-
	2N	80	8	8

sampled: Aat-2, Ak, Acon, Adh-1, Ck-B, Est-1, Est-2, Fum, Gpi-A, Gdh, Gapdh-1, G3pdh-B, Ldh-A, Ldh-B, Ldh-C, Mdh-A, Mdh-B, Mdh-m, Pro-1, Pro-3, Pro-5, and Xdh. The remaining 21 loci were polymorphic either within or between species (Table 2).

Genetic similarity values for the three pairwise comparisons (Table 3) were between 0.70 and 0.85, which is near the high end of the range of genetic similarity values found between congeneric fish species (Shaklee et al. 1982, Thorpe 1983). Nevertheless, each species pair can be distinguished on the basis of apparent fixed differences at multiple gene loci. The samples of *Paralabrax clathratus* and *P. nebulifer* shared no alleles at seven presumptive gene loci (Adh-2, Ck-A, G6pdh, Icdh-S, Pgdh, Pro-4, Sod); *P. clathratus* and *P. maculatofasciatus* were distinct at six loci (Ck-A,

Table 3
Values of genetic distance (above diagonal) and mtDNA nucleotide sequence differentiation (below diagonal) between three *Paralabrax* species. Standard errors of the estimates are in parentheses.

	P.c.	*P.n.*	*P.m.*
Paralabrax clathratus	-	0.304 (0.090)	0.265 (0.085)
Paralabrax nebulifer	0.145 (0.026)		0.165 (0.063)
Paralabrax maculatofasciatus	0.142 (0.027)	0.069 (0.019)	-

Est-3, Icdh-S, Pgdh, Pro-2, Sod); and *P. nebulifer* and *P. maculatofasciatus* were distinguished at six loci (Adh-2, Est-3, Gapdh-2, G6pdh, Pro-2, Pro-4). A number of loci were also identified that are capable of separating one species from each of the other two. For example, *P. clathratus* is fixed for alleles not found in *P. nebulifer* or *P. maculatofasciatus* at four gene loci (Ck-A, Icdh-S, Pgdh, Sod). Thus all three species can be distinguished using only two loci: one of the four for which *P. clathratus* has unique alleles, and one of the six that separates *P. nebulifer* and *P. maculatofasciatus*. A similar procedure can be used with the two loci (Adh-2, G6pdh) that distinguish *P. nebulifer* from the other two species or the two loci (Est-3, Pro-2) for which *P. maculatofasciatus* has unique alleles. No single locus was identified that by itself completely distinguishes all three *Paralabrax* species. The closest to a completely diagnostic locus is Ada; at this locus, a different allele predominates in each of the species at a frequency of 0.80 or more.

Considerable mtDNA sequence differentiation was demonstrated between the three *Paralabrax* species (Table 4). Six of the restriction endonucleases (*Bgl*II, *Cla*I, *Kpn*I, *Sal*I, *Sma*I, and *Xba*I) failed to cleave the circular mtDNA molecule more than once in each of three species and were therefore uninformative. Of the 13 restriction endonucleases which produced two or more fragments in the *Paralabrax* species, eight (*Ava*I, *Ava*II, *Bst*EII, *Hinc*II, *Hind*III, *Hinf*I, *Hpa*II, and *Xho*I) were able to distinguish all three species, while three enzymes (*Bam*HI, *Eco*RI, and *Sst*I) were able to distinguish one of the species from the other two, and two enzymes (*Pst*I and *Pvu*II) produced similar mtDNA fragments in all three species. Thus 8 of the 13 informative restriction endonucleases were diagnostic for all three species.

The mean nucleotide sequence divergences between the three *Paralabrax* species, in pairwise comparisons, are presented in Table 3. Because digestions with *Hinf*I, *Hpa*II, and *Ava*II (restriction endonucleases which recognize four or five nucleotide base pairs) produced so many fragments, it was not possible to assure homology of similarly migrating fragments, and the results from these enzymes were not used in the calculation of interspecific divergences.

Little intraspecific mtDNA nucleotide sequence variation was detected in this study. Of the 18 fish analyzed with the 13 informative restriction endonucleases, only two variants were encountered, each in a single individual (Table 4).

The species-specific fragment patterns produced from the digestion of *Paralabrax* mtDNA with the restriction endonuclease *Hind*III (Fig. 1) were considered the most practical to use for specific identification because there were diagnostic differences in the larger (most easily visualized) bands. Fresh or frozen tissue samples as small as 0.01 g could be identified from a *Hind*III digestion of the mtDNA enriched in a miniprep procedure and run on a 1.0% agarose minigel stained with ethidium bromide.

It was not possible to identify tissue samples smaller than 0.01 g on ethidium bromide-stained minigels

Table 4

Restriction fragment sizes (in kilobase pairs) in three species of *Paralabrax*. Not all fragments were resolved in digestions with *Ava*II.

Restriction endonuclease	*Paralabrax* species	Fragment sizes
*Ava*I	*clathratus*	7.4, 4.1, 2.1, 1.9
	maculatofasciatus	11.9, 2.6, 2.3
	nebulifer	9.2, 3.6, 2.7, 1.3
*Ava*II	*clathratus*	4.9, 2.7, 1.8, 1.2, 1.1, 0.7, 0.7, 0.5
	maculatofasciatus	2.6, 2.2, 1.7, 1.5, 1.5, 1.5, 1.3, 1.1, 1.0
	nebulifer	5.7, 1.9, 1.8, 1.5, 1.5, 1.3, 1.1, 1.0
*Bam*HI	*clathratus*	16.8
	maculatofasciatus	10.0, 6.8
	nebulifer	10.0, 6.8
*Bst*EII	*clathratus*	6.5, 5.3, 5.0
	maculatofasciatus	9.4, 7.4
	nebulifer	14.3, 2.5 (5) or 10.1, 4.2, 2.5 (1)
*Eco*RI	*clathratus*	8.8, 7.9
	maculatofasciatus	8.8, 7.9
	nebulifer	7.9, 4.6, 2.4, 1.9
*Hinc*II	*clathratus*	4.2, 2.8, 2.7, 2.4, 1.3, 1.2, 1.0, 0.7, 0.3
	maculatofasciatus	4.6, 3.6, 3.0, 2.7, 1.5, 0.7, 0.6
	nebulifer	4.0, 3.5, 3.0, 2.4, 1.6, 1.5, 0.7
*Hind*III	*clathratus*	6.2, 4.0, 2.2, 1.8, 0.7, 0.6
	maculatofasciatus	6.2, 4.7, 2.2, 2.0, 1.8
	nebulifer	6.2, 6.2, 2.2, 1.8, 0.4
*Pst*I	*clathratus*	12.6, 4.2
	maculatofasciatus	12.6, 4.2 (5) or 9.4, 4.2, 3.0 (1)
	nebulifer	12.6, 4.2
*Pvu*II	*clathratus*	11.6, 5.2
	maculatofasciatus	11.6, 5.2
	nebulifer	11.6, 5.2
*Sst*I	*clathratus*	14.0, 2.8
	maculatofasciatus	16.8
	nebulifer	16.8
*Xho*I	*clathratus*	12.1, 2.9, 1.8
	maculatofasciatus	16.8
	nebulifer	9.8, 4.8, 2.2

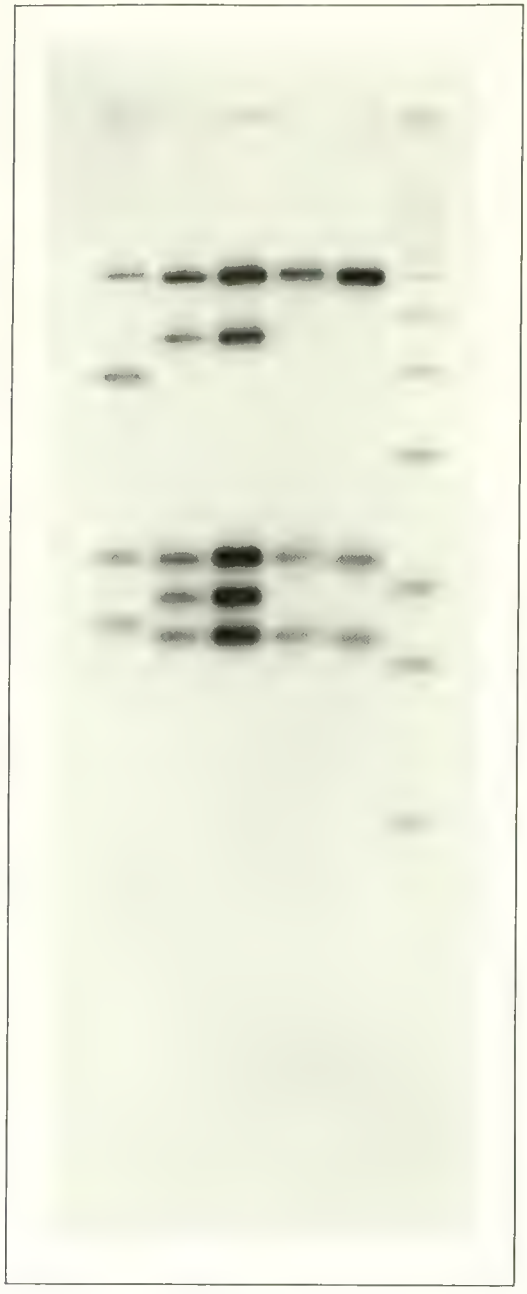

Figure 1

Species-specific fragment patterns of mtDNA isolated from three species of *Paralabrax* and digested with the restriction endonuclease *Hind* III. Note that the upper (larger) bands distinguish the three species. From left to right: *P. clathratus* (1), *P. maculatofasciatus* (2), *P. nebulifer* (2), and the size standard (BRL 1 Kb ladder). The mtDNA restriction fragments were endlabeled with radioactive nucleotide triphosphates, separated on a 1.0% agarose gel and visualized by autoardiography.

Figure 2

A Southern blot of *Hind* III digests of genomic DNA isolated from individual *Paralabrax* eggs and probed with biotinylated *Paralabrax* mtDNA. The eggs can easily be identified on the basis of the fragment patterns by comparison with those in Figure 1. One preparation (lane 5) did not contain sufficient DNA for identification. From left to right: *P. maculatofasciatus* (2), *P. nebulifer* (2), and *P. clathratus* (1).

because there was not sufficient mtDNA for visualization of the restriction fragments. However, samples as small as 0.6 mg (one *Paralabrax* egg) could be identified after Southern transfer and hybridization with a biotinylated probe (Fig. 2). Although greater sensitivity could have been obtained with a radioactively labeled probe, the results obtained with the biotinylated probe were sufficient to identify an individual fresh or ethanol preserved egg, and avoided the cost and problems of probe half-life and waste disposal associated with radioactively labeled probes.

Discussion

The results of the electrophoretic and mtDNA analyses are similar in several respects. First, the absolute level of genetic differentiation between the *Paralabrax* species is relatively small and is consistent with values typically found between other closely related organisms (Avise and Aquadro 1982, Ferris and Berg 1987). Second, the comparison of *P. maculatofasciatus* and *P. nebulifer* yields the smallest genetic distance of the three pairwise comparisons.

A major focus of the electrophoretic and mtDNA analyses was to find a biochemical character which would unambiguously differentiate the early-life-history stages of the three *Paralabrax* species found in southern California coastal waters. The electrophoretic investigation revealed several apparently fixed allelic differences between any two of the three species and demonstrated that a screening of a minimum of two electrophoretic loci will result in a positive specific identification. This methodology can be used to identify late larvae, juveniles, or adults in which there is sufficient tissue (or enzyme activity) to survey two or more loci. However, it was not always possible to score the diagnostic loci in *Paralabrax* eggs and larvae smaller than 10 mm total length. Although it may have been possible to improve the resolution of the electrophoretic techniques, we chose to rely upon mtDNA restriction fragment differences to identify *Paralabrax* eggs and early larvae.

The restriction endonuclease analysis of *Paralabrax* mtDNA, like the electrophoretic survey, demonstrated considerable genetic differentiation among the three species. Several restriction endonucleases were each capable of distinguishing the three species of basses. Furthermore, the mtDNA analysis not only worked with relatively large adult tissue samples, but with quantities as small as an individual egg. Consequently, the mtDNA analysis is the method of choice for the identification of *Paralabrax* early-life-history stages.

Several ecological and assessment studies involving *Paralabrax* eggs and early larvae have not been possible because of an inability to specifically identify the early-life-history forms. The mtDNA isolation and analysis techniques presented in this paper will facilitate such studies. Furthermore, because the methods work with ethanol-preserved as well as fresh specimens, there is no need to separate *Paralabrax* eggs and larvae from a fresh plankton tow while at sea.

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Abstract.– Atlantic spadefish *Chaetodipterus faber* were collected from South Carolina between July 1985 and May 1987 to examine feeding habits, age and growth, and reproduction. Analysis of stomach contents by habitat showed that fish from estuarine areas and offshore artificial reefs ate mainly hydroids, while Anthozoa were dominant food items for fish from nearshore marine areas. Stomach contents from fish obtained by hook-and-line near offshore artificial reefs, using *Stomolophus meleagris* as bait, indicated that scyphozoan jellyfish were the dominant prey, but fish collected by spear or net had stomach contents dominated by hydroids, anthozoans, and polychaetes. Ages of Atlantic spadefish were determined from whole sagittae. Marginal increment analysis indicated that annuli formed between December and May. The von Bertalanffy growth equation, derived from back-calculated mean total lengths at age was $l_t = 490(1-e^{-0.34(t+0.18)})$, where t is age in years, and l_t = total length at age. Mean asymptotic total length was calculated to be 490 mm. The oldest fish examined was age 8 and 504 mm TL. Histological examination indicated that fish matured at age 1 and spawned from May through August.

Feeding Habits, Age, Growth, and Reproduction of Atlantic Spadefish *Chaetodipterus faber* (Pisces: Ephippidae) in South Carolina*

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The Atlantic spadefish *Chaetodipterus faber* (Broussonet) is the only member of the family Ephippidae native to the western Atlantic Ocean. This species inhabits coastal waters from Chesapeake Bay to southeastern Brazil, including the Gulf of Mexico (Johnson 1978), and has also been introduced into the waters surrounding Bermuda (Burgess 1978). It is a common fish in South Carolina, particularly from early spring through late fall, and all life stages have been collected in South Carolina.

Since 1978 the Recreational Fisheries Section of the South Carolina Wildlife and Marine Resources Department (SCWMRD) has promoted *C. faber* as a sportfish, primarily due to the attraction of large numbers of adult Atlantic spadefish to offshore artificial reefs that have been created and/or maintained by SCWMRD. Atlantic spadefish have traditionally been a relatively minor recreational species in South Carolina and were only occasionally caught by hook-and-line fishermen using shrimp or squid as bait. Observations of feeding behavior by SCWMRD personnel in the early 1980s suggested that Atlantic spadefish might eat *Stomolophus meleagris*, the cannonball jellyfish. As a result, a technique using cannonball jellyfish as bait was developed and has proven extremely effective in attracting and capturing *C. faber* (Moore et al. 1984). This method has since been the subject of some recreational fishing publications (Ogle 1985, 1987). Little, however, is known about the life history, feeding habits, age and growth, or reproductive biology of *C. faber*, even though such information is preliminary to proper assessment and management.

The present study was undertaken with three major objectives. The first was examination of stomach contents from specimens of *C. faber* in order to describe the diet. In addition to a qualitative and quantitative diet analysis, I wished to determine if the mode of collecting fish (hook-and-line vs. net and spearfishing) might bias the results of diet analysis. Since Atlantic spadefish appeared to inhabit different areas depending upon body size and age, I also wished to determine if ontogenetic and habitat differences existed in the diets of the fish collected. The second portion of the study dealt with age and growth of Atlantic spadefish in South Carolina by finding a suitable ageing method and estimating growth rates. The final segment of the research explored the reproductive biology of *C. faber*, specifically determination of spawning period, sex ratios, and the age at sexual maturity of Atlantic spadefish off South Carolina.

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Materials and methods

Data collection

Specimens were collected July 1985 through May 1987, excluding the periods from December 1985–April 1986 and December 1986–April 1987 when Atlantic spadefish were absent from collection sites (Fig. 1). Most of the specimens less than 200 mm total length were provided by other research programs which obtained them as bycatch in trawl tows.

Collections were from three different habitat strata (Fig. 1). Stratum 1 included estuarine habitats. The fish in this stratum were primarily young-of-the-year and were collected by a variety of gear, including dipnets, seines, stopnets, and trawl nets. Stratum 2 consisted of shallow nearshore habitats less than 20 m in depth with bottoms consisting primarily of mud or sand and shell, with rare patches of live bottom (sponges and soft corals, low rock relief). The fish in stratum 2 were all collected by trawling. Stratum 3 contained fish collected primarily by spearfishing while SCUBA diving on artificial reefs located off South Carolina's coast and on the Murrell's Inlet jetties. Some specimens from the artificial reefs were collected by hook-and-line using *Stomolophus meleagris* as bait. The artificial reefs and the jetties were similar habitats in that all were man-made structures providing relatively high relief and all were covered with a variety of fouling organisms such as algae, sponges, corals, hydroids, sea anemones, bryozoans, and ascidians. The fish from stratum 3 were all adults.

Fish ($n = 832$), subsampled from 84 collections, were sexed, weighed to the nearest gram, and total length (TL) and standard length (SL) measured to the nearest millimeter. Subsamples, consisting of 177 stomachs and 233 gonads, were excised from a representative portion of the collections, preserved in buffered 10% seawater formalin, and later transferred to 50% isopropanol. Otoliths (sagittae) were removed from 643 specimens and stored in 95% ethanol.

Stomach contents

Stomachs of *Chaetodipterus faber* are well-defined structures, and contents of the digestive tracts between the pharynx and the pyloric sphincter were examined using compound and stereoscopic microscopes. Stomachs were scored for fullness and food items were sorted, identified to the lowest practical taxa, and counted. Colonial organisms, such as hydroids and bryozoans, and multiple fragments of individual species were counted as single individuals unless numbers could be estimated from the fragments by counting structures such as eyes or legs. After removing excess water by blotting on absorbent paper, the volume of

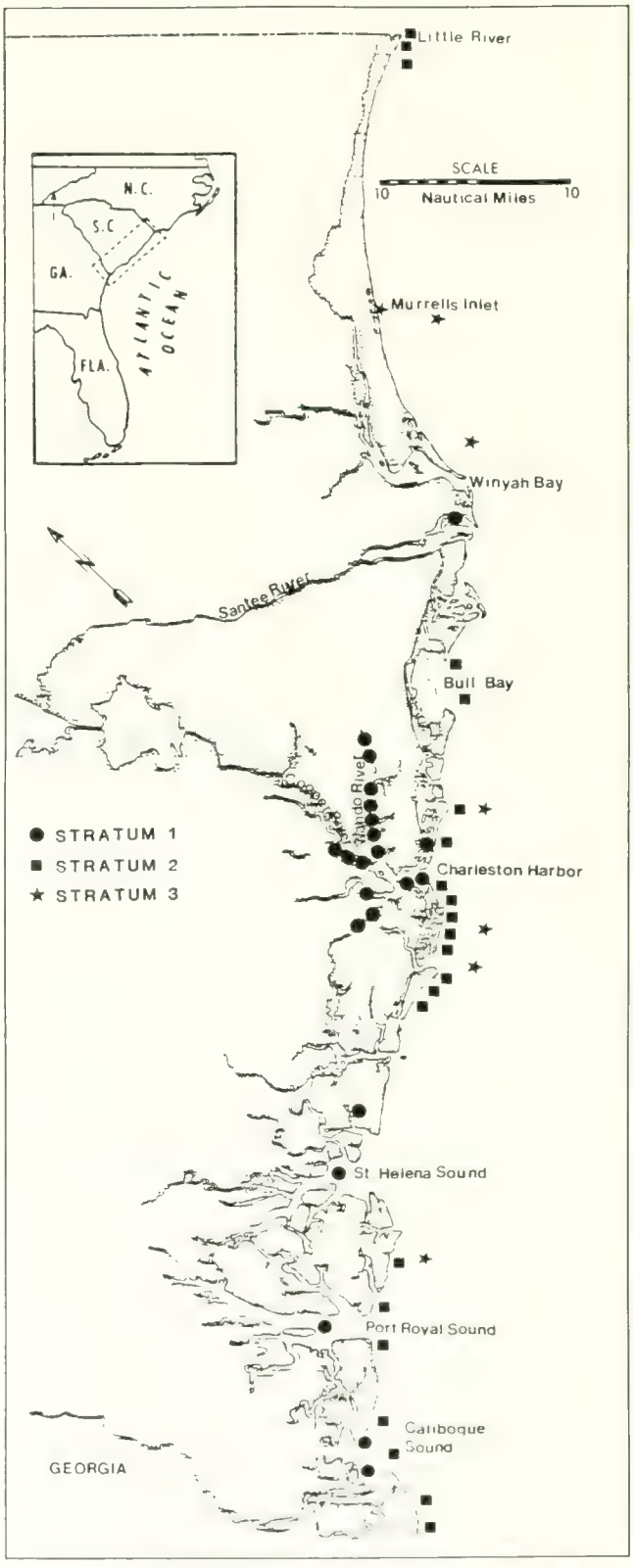

Figure 1

Positions of collection sites in South Carolina for *Chaetodipterus faber*. Symbols indicate general collection areas, and some indicate more than one collection in a particular area. Circles (●) represent estuarine sites (stratum 1), squares (■) represent shallow nearshore sites with sandy bottoms (stratum 2), and stars (★) represent artificial reef habitats (stratum 3).

each taxon was determined by displacement, except in the case of small items. Volumes of small items were estimated using a 1 × 1 mm grid. Percent frequency of occurrence (%F), percent of total number (%N), and percent of total volume (%V) of stomach contents were calculated by higher taxonomic categories for the entire data set and for the data separated by length intervals and collection strata, and these values were used to calculate an index of relative importance (*IRI*) (Pinkas et al. 1971):

$$IRI = (\%N + \%V) \times \%F.$$

Shortly after laboratory analysis of stomach contents commenced, it became apparent that most of the prey items observed were either colonial or fragments of soft-bodied organisms that could only be counted as one individual per stomach each time they were encountered. The primary countable organisms were amphipods and copepods, which were present in large numbers, but accounted for only a small portion of the volume. In the opinion of some researchers (Lagler 1956, Crow 1982), percent number can lead to a somewhat distorted view if small organisms are present in large numbers even though they are of minor importance to the diet of a fish. Consequently, a modified index (*MI*) of relative importance which did not incorporate %N into the formula was also calculated for each taxonomic category:

$$MI = \%F \times \%V.$$

Stomach contents from 27 fish taken by hook-and-line were analyzed separately in the above manner and compared with the data from fish collected by nets and spearfishing.

Age and growth

Sagittae were chosen as structures for age determination since they were easily accessible, easily stored, and exhibited well-defined growth zones. Other structures were deemed unsuitable as ageing structures for various reasons. Scales were small, frequently regenerated, and the marks on them were considerably more difficult to interpret than those on the sagittae. Vertebrae were difficult to obtain and time-consuming to prepare for analysis.

No differences were observed between the left and right sagittae of individual fish and, unless damaged or unavailable, the left sagitta was used in age analysis. Cleaned whole sagittae were examined using both reflected and transmitted light, as necessary, in order to establish the location of presumed annuli. Whole otoliths were used since 100% agreement was obtained between counts of opaque zones from a subsample ($n = 18$) of otolith sections and counts from the corresponding whole otoliths. Sagittae were placed, concave-side-up, in a dish containing cedar oil and viewed with reflected light against a dark background at 25× using a stereoscope equipped with an ocular micrometer (1 ocular unit = 0.04 mm). The distance (in ocular units) from the kernel to each opaque mark and from the outermost mark to the edge of the sagitta (marginal increment) was determined from measurements made along the ventral radius of each sagitta (Fig. 2). These measurements were performed on two occasions separated in time by at least 2 weeks, and the two sets of measurements were compared to see if otolith measurements were repeatable.

Both least-squares linear regressions (Sokal and Rohlf 1981) and geometric mean (GM) functional regressions (Ricker 1973, Sokal and Rohlf 1981) were used to describe the relationship of TL to ventral otolith radius (OR), SL to TL, and lengths to weight. Mean back-calculated TL at age was derived by the Fraser-Lee method using the intercept of the OR-TL relationship (Poole 1961, Carlander 1982). Mean back-calculated TLs were weighted by the reciprocal of the standard error of the mean squared, and the von Bertalanffy growth equation (Bertalanffy 1938) was then fitted to mean back-calculated TL at age by using the SAS NLIN procedure while employing Marquardt's algorithm and the SAS NLIN weight statement (Helwig and Council 1979).

Reproduction

Reproductive tissues were processed in an Auto-Technicon 2A Tissue Processor, vacuum infiltrated, blocked in paraffin, and sectioned (6–10 μm thick) on a rotary microtome. Sections were stained with Harris hematoxylin and counter-stained with eosin-Y. Mounted sections were then examined with a compound microscope, and sex and maturity stages were assigned according to the criteria of Waltz et al. (1979). The ratio of males to females and maturity stages by month were examined to determine sex ratios and spawning period of *C. faber* off South Carolina.

Results

Analysis of stomach contents

Eighty percent of the stomachs obtained by hook-and-line contained food, and at least seven prey species

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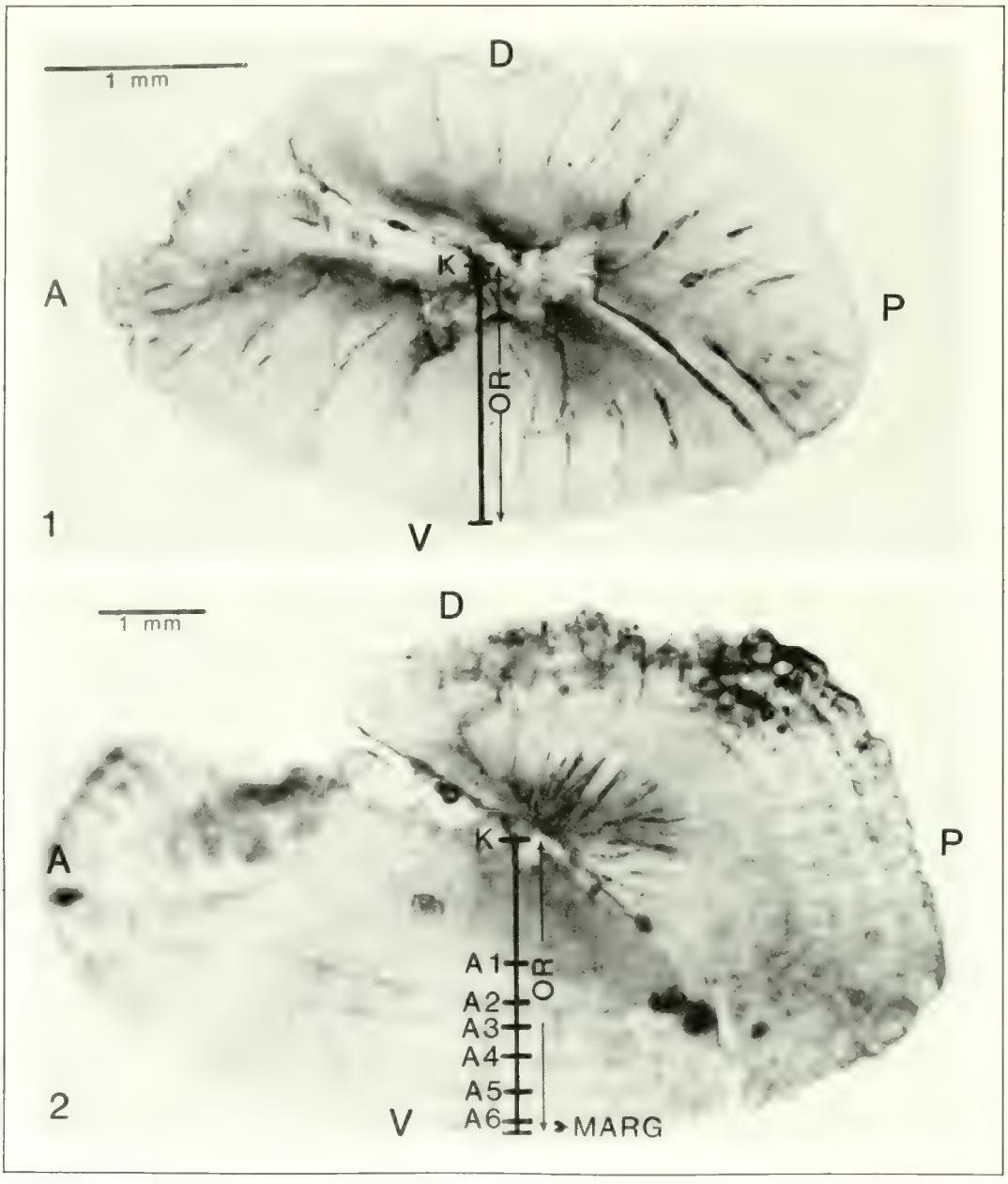


Figure 2

Measurements taken from each sagitta of *Chaetodipterus faber* used in age analysis. (1) Photograph of the left sagitta from a young-of-the-year (115 mm TL) specimen. (2) Photograph of a whole left sagitta from an age-6 (396 mm TL) specimen. Orientation of the sagittae within the neurocranium is indicated: A anterior; P posterior; D dorsal; V ventral. A1–A6 represent successive measurements to each annulus; OR is the ventral sagitta radial measurement; MARG is the marginal increment; K is the kernel of the sagitta.

were present (Table 1). *Stomolophus meleagris* was, by far, the dominant organism according to all numeric indicators (%*F*, %*N*, %*V*, *IRI*, and *MI*). Hydroids, epifaunal amphipods, and anthozoans (sea anemones) were observed in considerably lower volumes, numbers, and frequencies than *S. meleagris*.

Ninety percent of the stomachs from Atlantic spadefish obtained by other collection methods (nets and spearing) contained food, and at least 75 prey species were represented (see Appendix). In sharp contrast to the hook-and-line samples, jellyfish occurred in only one stomach collected by nets or spearing even though *S. meleagris* and other jellyfish were common in the artificial reef areas during many of the spearfishing expeditions and were abundant in trawl catches. Furthermore, the species of jellyfish eaten was identified, by

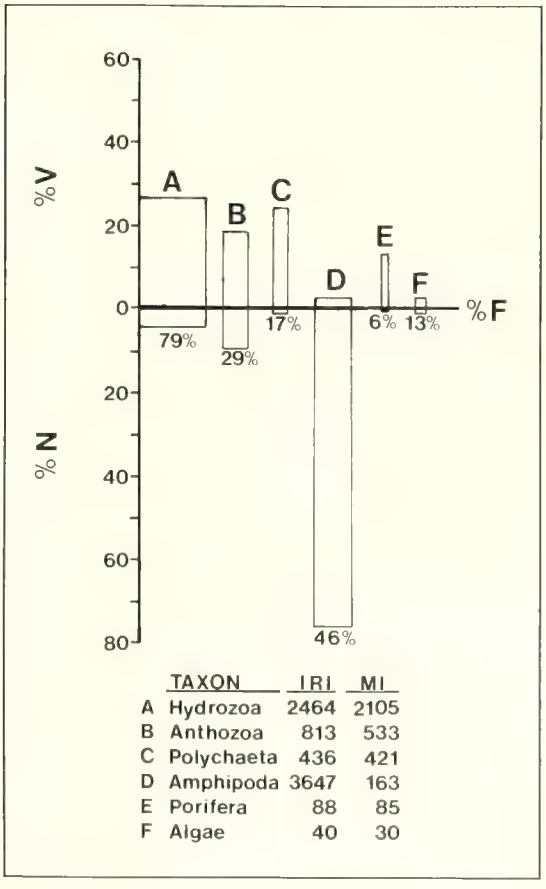
Table 1

Percent frequency of occurrence (%*F*), percent of total number (%*N*), percent of total volume (%*V*), index of relative importance (*IRI*), and modified index of importance (*MI*) for food items of *Chaetodipterus faber* obtained by hook-and-line in South Carolina using *Stomolophus meleagris* as bait.

Prey item	%*F*	%*N*	%*V*	*IRI*	*MI*
Cnidaria					
Hydrozoa					
Eudendrium sp.	18.18	9.52	0.69	185.62	12.54
Obelia sp.	4.55	2.38	0.01	10.88	0.05
Hydrozoa undetermined	4.55	2.38	0.04	11.03	0.18
Total Hydrozoa	27.27	14.29	0.74	409.67	20.17
Anthozoa					
Actiniaria	4.55	2.38	0.55	13.33	2.50
Scyphozoa					
Stomolophus meleagris	95.45	50.00	98.66	14,189.60	9417.10
Crustacea					
Amphipoda					
Caprella penantis	13.64	19.05	0.03	260.25	0.41
Erichthonius brasiliensis	9.09	9.52	0.01	86.63	0.09
Jassa falcata	4.55	4.76	<0.01	21.67	0.01
Total Amphipoda	27.27	33.33	0.04	910.12	1.09

Number of stomachs examined: 27

Examined stomachs with food: 22



examining tentacle arrangement and nematocyst morphology, as *Chiropsalmus quadrumanus*, a cubomedusa known as the sea wasp. In stomachs obtained by nets and spearing, hydroids were dominant by volume (27%) and were the most frequently observed organisms (seen in about 80% of the stomachs examined) (Fig. 3). Amphipods were in 45% of the stomachs and accounted for about 76% of the individual organisms, but had a low volume (4%). Nearly all of the amphipods were epifaunal, species primarily caprellids and tubicolous gammarids, that are frequently associated with hydroids. Anthozoans, consisting nearly equally of anemones (Actiniaria) and sea pansies *Renilla reniformis* were present in 29% of the stomachs, accounted for 10% of the individuals, and were the third-ranking taxon in terms of percent volume. Polychaetes were seen in 17% of the stomachs and accounted for 24% of total volume, but comprised less than 1% of the number of individuals. This category consisted primarily of terebellid feeding tentacles, which were probably cropped by *C. faber*

Figure 3

Percent frequency (%*F*), percent number (%*N*), percent volume (%*V*), index of relative importance (*IRI*), and modified index of importance (*MI*) for higher taxonomic groups of food in the diet of *Chaetodipterus faber* collected in South Carolina waters by nets and spearing.

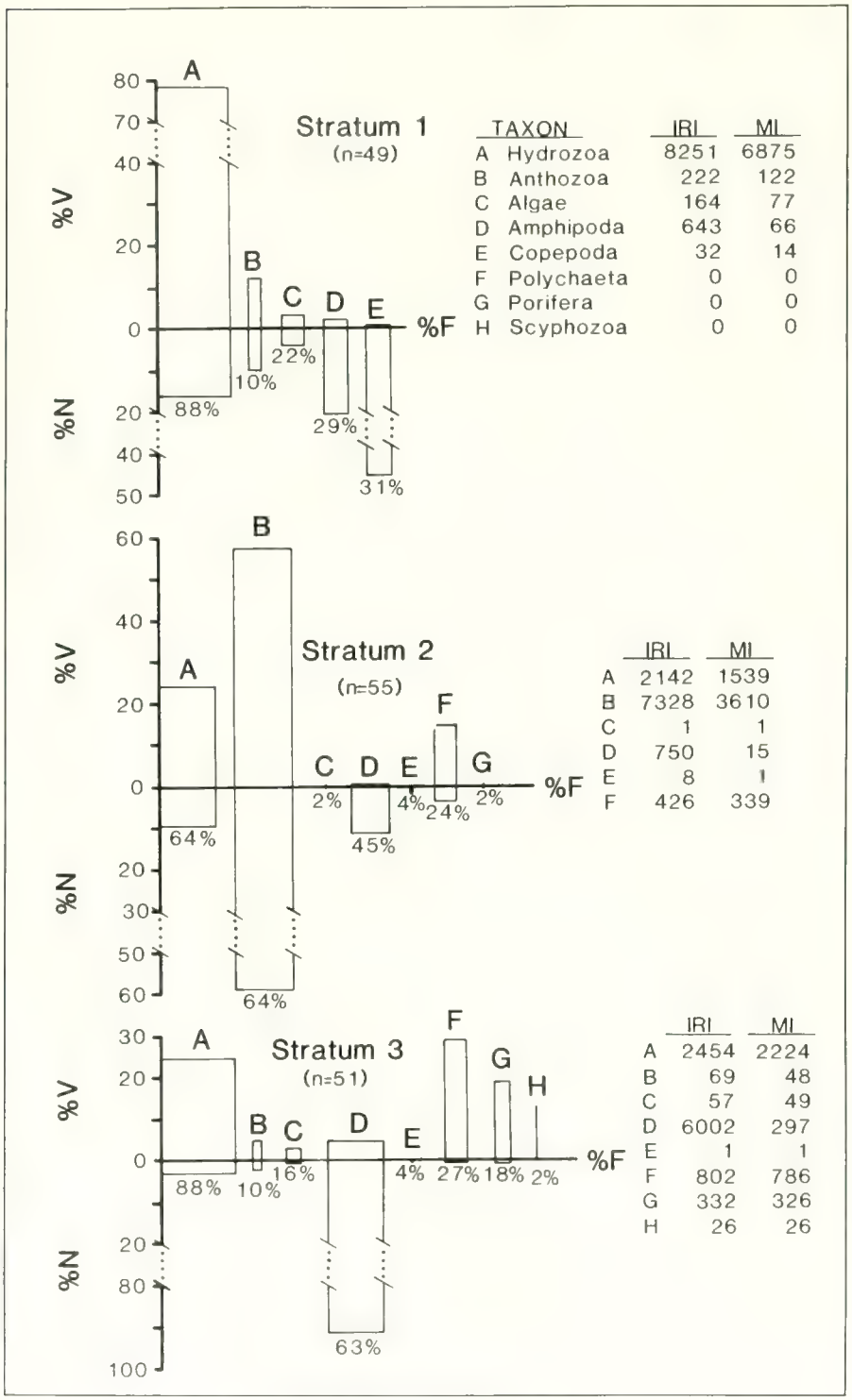


Figure 4

Percent frequency (*%F*), percent number (*%N*), percent volume (*%V*), index of relative importance (*IRI*), and modified index of importance (*MI*) for higher taxonomic groups of food in the diet of *Chaetodipterus faber* collected in South Carolina waters, by strata. Stratum 1 is composed of inshore estuarine habitats; stratum 2 encompasses shallow (<20 m), nearshore habitats with sandy bottoms; stratum 3 includes offshore artificial reef areas and the Murrells Inlet jetties.

while these polychaetes were feeding. Since heads or mouthparts of the polychaetes were usually absent, there were often no countable body parts, making it impossible to determine the number of individuals eaten. I had similar problems in enumerating hydroids, sponges, algae, bryozoans, and occasionally sea anemones and sea pansies. The *IRI* ranked amphipods as the dominant prey, followed by hydroids, anthozoans, polychaetes, and sponges. The *MI* ranked hydroids as the most important taxon, followed by anthozoans, polychaetes, amphipods, and sponges.

Hydroids were the dominant food item for fish from stratum 1, as shown by both the *IRI* and the *MI* (Fig. 4). Less important were anthozoans, algae, amphipods

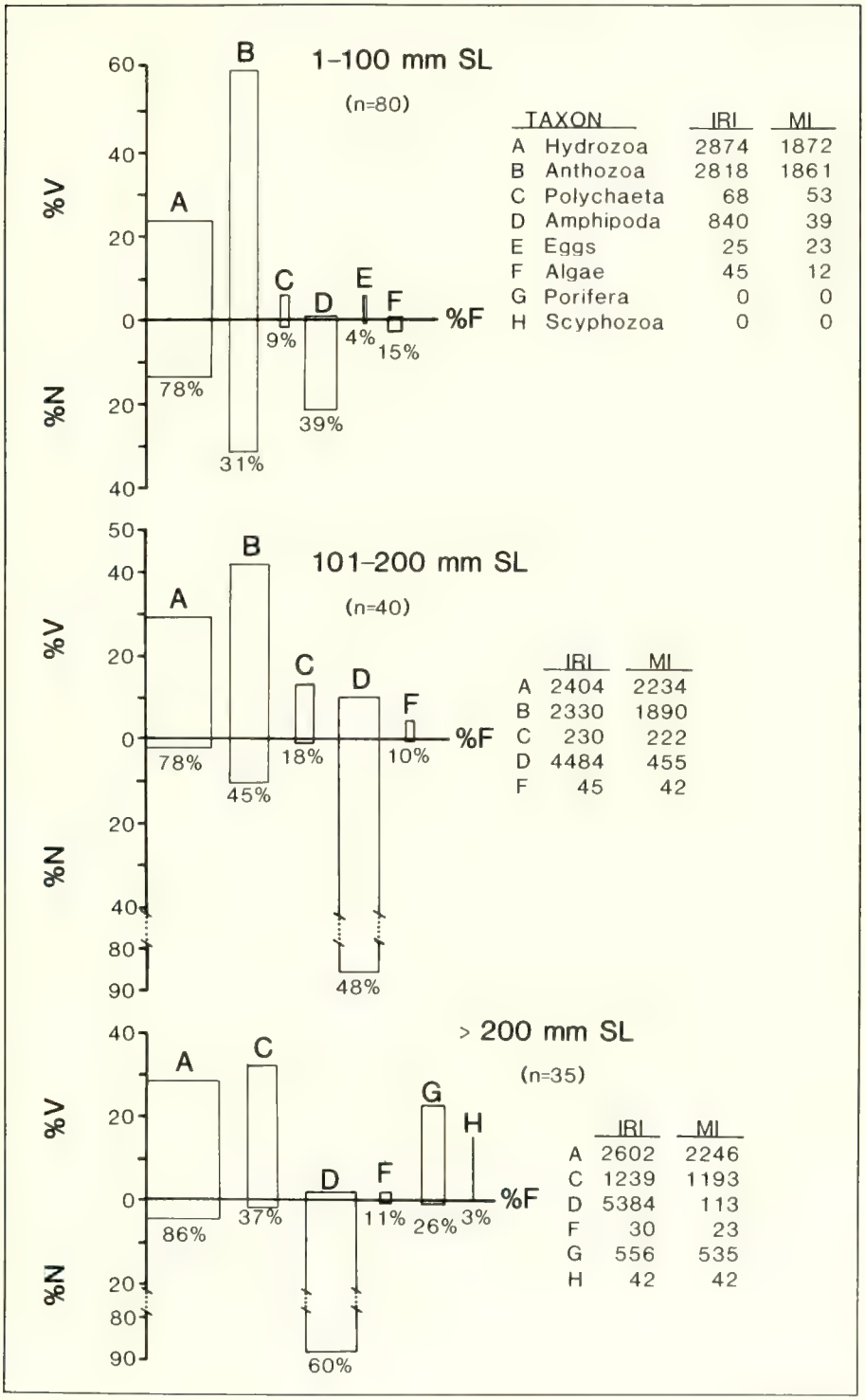


Figure 5

Percent frequency (%*F*), percent number (%*N*), percent volume (%*V*), index of relative importance (*IRI*), and modified index of importance (*MI*) for higher taxonomic groups of food in the diet of *Chaetodipterus faber* collected in South Carolina waters, by standard length (SL) intervals.

and copepods. In stratum 2, the relative-importance indices indicated anthozoans were the major component of the diet, followed by hydroids. Anthozoans in stomachs of fish from stratum 2 consisted mainly of *Renilla reniformis*. Jellyfish (Scyphozoa) were never seen in stomachs of fish from stratum 1 or stratum 2. The *IRI* indicated that amphipods were the most important prey in stratum 3, while the *MI* ranked hydroids as the dominant food item. Amphipods composed 91% of the individuals and were found in 63% of the stomachs containing food, but accounted for only 5% of total volume of food in stomachs from stratum 3. Hydroids, on the other hand, were observed in 88% of the stomachs from stratum 3 which contained food and

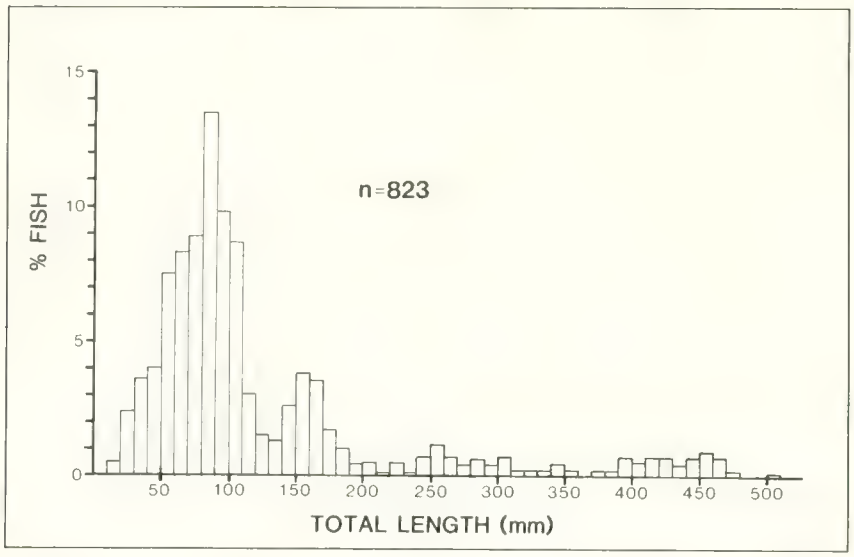


Figure 6
Percent frequency of *Chaetodipterus faber* within 10-mm TL size classes.

composed 25% of total volume in stratum 3. Percent number was low for hydroids in stratum 3, but they could only be counted as one individual per stomach each time they were encountered, whereas there were usually many amphipods per stomach. The *IRI* ranked hydroids as the second-most important food source, followed by polychaetes (feeding tentacles) and sponges. The *MI* ranked polychaetes second, followed by sponges and amphipods. Although Scyphozoa ranked as one of the top seven food items in stratum 3, it occurred in only one stomach, which was distended with 16 mL (after blotting) of jellyfish. Most stomachs from stratum 3 that were considered full contained 3–6 mL of food.

The *MI* indicated that hydroids were the dominant food for all size classes of *C. faber*, being found in over 75% of the stomachs from each size class and accounting for approximately 25% of the volume in each of the groups (Fig. 5). The *MI* also showed that anthozoans were nearly as important as hydroids for fish up to 200 mm SL, but were not important to fish >200 mm SL. The second-ranking prey for fish >200 mm SL was polychaete-feeding tentacles according to the *MI*. The *IRI* denoted amphipods as a major source of food for fish of all sizes (dominant, by far, for fish >100 mm SL), but this was certainly due to the numerical bias of the *IRI*. The *MI* indicated amphipods were a minor dietary component except for fish 100–200 mm SL, where they were the third-most important prey. Unidentified egg masses, probably gastropod eggs, were found in 4% of the stomachs from fish up to 100 mm, but were a relatively minor component of the diet from fish this size. Sponges were observed in 26% of the stomachs from fish >200 mm SL and accounted for 21% of total volume of prey for these fish, making it the third-ranked food item for fish in this group according to the *MI*.

Age and growth

All but 6 of the 643 pairs of otoliths obtained were used in age analysis, since 6 pairs were deemed unreadable due to deformities in otolith structure. Discernment of check marks on whole otoliths of *C. faber* was relatively easy in either reflected or transmitted light, and there was 93% agreement between the two series of counts and measurements. The differences between the remaining 7% (attributable to measurement and recording errors) were satisfactorily resolved, allowing all 637 otolith pairs to be utilized in ageing analysis. The pattern of alternating opaque and translucent bands which were observed on the sagittae were believed to be permanent records of the physiological growth of the Atlantic spadefish from which they had been obtained.

Length-frequency distributions are often used to separate fish of different lengths into age groups and are also utilized to validate ageing techniques, particularly for younger age groups (Lagler 1956, MacDonald 1987). Good agreement was seen between the TLs of fish determined to be age 0 and age 1 by counting opaque zones on otoliths and the range of TLs for the first and second groups in a length-frequency distribution (Fig. 6). Consequently, the innermost opaque zone on each sagitta was believed to be the first annulus.

Since marginal increments on the otoliths should approach zero during the time of annulus formation, the monthly means were calculated to determine if one opaque band was laid down on the sagittae during each year. Generally, the mean marginal increment was lowest in May and increased steadily, by month, through

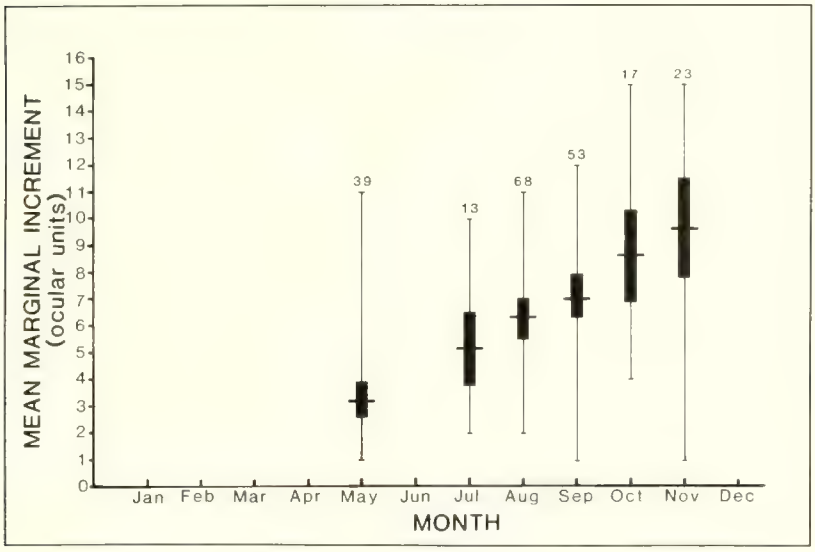


Figure 7

Mean marginal increments, in ocular units, on the otoliths of *Chaetodipterus faber* by month of capture in South Carolina. Heavy horizontal bars represent mean values, heavy vertical bars represent 95% confidence intervals, and vertical lines represent ranges of measurements. Numbers over each series of values are sample sizes.

Table 2

Sample sizes (n), means ($\bar{x}$), and standard deviations (SD) for observed lengths (mm), and weight (g) by age for *Chaetodipterus faber*.

	Total length			Standard length			Weight		
Age	n	($\bar{x}$)	SD	n	($\bar{x}$)	SD	n	($\bar{x}$)	SD
0	421	84	24	424	67	20	424	30	21
1	121	163	21	121	133	17	121	185	74
2	36	265	29	36	216	25	36	670	202
3	21	309	43	21	250	36	21	1063	469
4	10	396	61	10	332	53	10	2107	810
5	17	440	27	17	367	24	17	3025	586
6	7	439	34	7	369	30	7	3087	867
7	0	–	–	0	–	–	0	–	–
8	1	472	–	1	405	–	1	–	–

November (Fig. 7). Although a marginal increment of zero was never observed, there was a strong indication that the opaque zones on the sagittae formed once a year between December and April, and, therefore, justified their use as annular marks. However, these were months when Atlantic spadefish were absent from collection sites and, consequently, no specimens were obtained.

The oldest fish was age 8, although no age-7 fish were collected. Observed mean lengths (TL and SL) and weight increased with age (Table 2), and all least-squares regression relationships were very highly significant ($P<0.001$) (Table 3). Analysis of the age composition of Atlantic spadefish by stratum showed that all fish taken in stratum 1 were young-of-the-year (age 0) and the fish from stratum 2 were predominantly age 1, although age-0 fish were seen in stratum 2 in increasing numbers from late summer to late fall. All fish taken on the artificial reefs (stratum 3) were age 2 or older.

Mean back-calculated TLs at age were lower than mean observed TLs for all age groups Mean back-calculated lengths at preceding annuli, weighted mean back-calculated lengths, and growth increments for all fish age 1 and older are in Table 4. Growth rates differed little between sexes. The von Bertalanffy growth equation, derived from back-calculated mean total lengths at age was:

$$l_t = 490(1 - e^{-0.340(t+0.18)}),$$

where t is age in years and l_t is total length at age (Table 5). There was good agreement between the mean observed, mean back-calculated, and theoretical

Table 3

Least-squares linear and geometric mean (GM) regression equations of weight (WT) on total length (TL) and standard length (SL), length-length, and TL-ventral otolith radius (OR) for *Chaetodipterus faber* from South Carolina waters. Weight unit in grams, SL and TL units in millimeters, and OR expressed as ocular units (1 ocular unit = 0.04 mm). All least-squares linear regressions were significant at $P<0.001$.

Least-squares equation	n	r^2	GM functional equation
$\log_{10}$ WT = −10.10 + 2.98 $\log_{10}$ TL	815	0.99	$\log_{10}$ WT = −10.17 + 3.00 $\log_{10}$ TL
$\log_{10}$ WT = −9.08 + 2.90 $\log_{10}$ SL	823	0.99	$\log_{10}$ WT = −9.16 + 2.92 $\log_{10}$ SL
TL = 3.9 + 1.2 SL	823	0.99	TL = 3.8 + 1.2 SL
SL = −3.1 + 0.8 TL	823	0.99	SL = −3.2 + 0.8 SL
TL = 14.1 + 0.1 OR	634	0.93	TL = 13.5 + 0.1 OR

Table 4

Mean observed and back-calculated total lengths (mm) at preceding annuli for *Chaetodipterus faber*.

Age (years)	Number of specimens	Mean length at capture	Mean back-calculated lengths at preceding annuli							
			I	II	III	IV	V	VI	VII	VIII
1	121	163	112							
2	36	265	125	195						
3	21	309	128	199	274					
4	10	396	162	236	305	361				
5	17	440	168	251	317	374	414			
6	7	439	132	210	278	338	383	417		
7	0	–	–	–	–	–	–	–	–	
8	1	472	186	230	302	356	382	409	436	454
		Weighted mean	123	213	294	363	404	416	436	454
		Growth increment	123	89	81	69	41	12	20	18

Table 5

Estimated parameters, their standard errors (SE), and 95% confidence limits (CL) of the von Bertalanffy growth equation for *Chaetodipterus faber*. Weighted residual sums of squares = 424.80; L_∞ is the mean asymptotic total length; K is the growth coefficient; and t_0 is the time (years) at which total length would theoretically be zero.

Parameter	Estimate	Asymptotic SE	Asymptotic 95% CL Lower	Asymptotic 95% CL Upper
L_∞	490.41	15.21	451.31	529.50
K	0.34	0.03	0.25	0.42
t_0	0.18	0.11	−0.11	0.48

TLs at age (Fig. 8). A mean asymptotic TL (L_∞) of 490 mm may be reasonable for fish off South Carolina. The largest recorded *C. faber* landed in South Carolina to date, which was captured and examined during the course of this study, measured 504 mm TL.

Reproduction

Chi-square tests of the ratios of males to females indicated that there were no significant ($P>0.05$) deviations from 1♂:1♀ ratios for *C. faber* of all ages combined or for fish grouped by ages 0–6.

Histological examination of reproductive organs revealed that 64% of age-0 males were mature and all males age 1 and older were mature. The smallest spent male was age 0 and 94 mm TL. Ovaries of all age-0 females were immature, while all females age 1 and older were mature. The smallest spent female was 120 mm TL.

Analysis of maturity stages by month indicated spawning activity for *C. faber* lasted from May through September, and the greatest percentage (97%) of developing and ripe gonads was observed in May (Fig. 9). From June to October the percentage of developing and ripe gonads decreased steadily to 0%. All reproductive organs from fish captured in October and November were resting, and no developing gonads were collected after August. Collapsed follicles in various

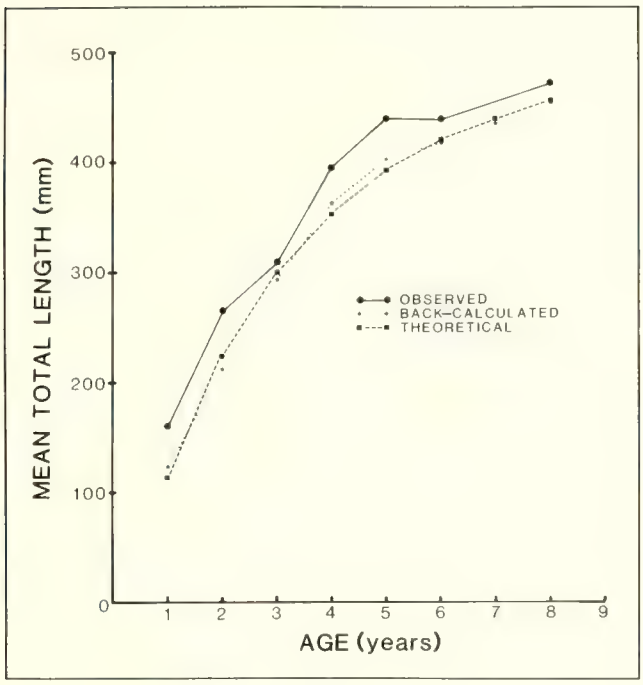


Figure 8

Mean observed, mean back-calculated, and theoretical (von Bertalanffy) total lengths (mm) at age for both sexes of *Chaetodipterus faber* from South Carolina waters.

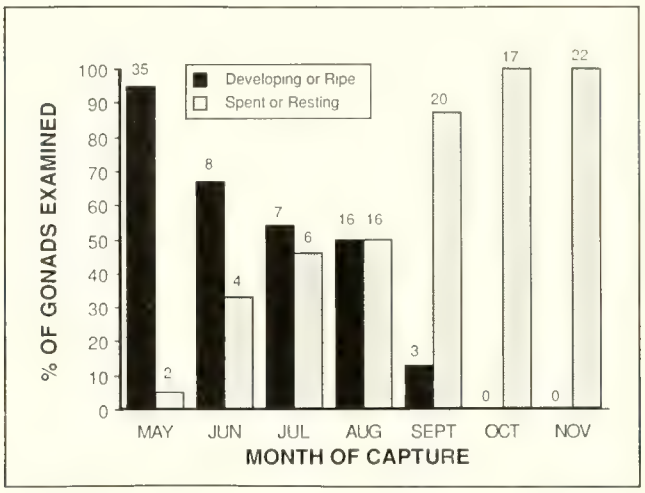


Figure 9

Maturity stages of age-1 and older *Chaetodipterus faber*, by month of capture in South Carolina waters, to illustrate spawning period. Fishes were grouped according to those with gonads that were developing or ripe and those with gonads that were spent or resting. Numbers over bars are sample sizes.

states of atresia were observed in some histological sections of ovaries which also contained developing oocytes, indicating that some serial spawning took place during the period May–August.

Discussion

Analysis of stomach contents

Dietary analysis indicated that *Chaetodipterus faber* in South Carolina eat mostly hydroids, anthozoans such as sea anemones and sea pansies, and polychaete tentacles. Pearce and Stillway (1976) reported the presence of an unusual fatty acid in the liver of *C. faber*. Since coelenterates appear to be the source of this fatty acid in certain fishes and marine turtles, the authors suggested that the elevated levels in Atlantic spadefish could be a reflection of a high dietary intake of coelenterates. Gallaway et al. (1981) believed that the hydroids and other fouling organisms they observed in the stomachs of Atlantic spadefish were being taken from the water column after being sloughed off the understructure of oil platforms. My underwater observations while SCUBA diving provided no evidence that Atlantic spadefish are primarily planktivores as suggested by Gallaway et al. (1981) and I never observed anything to suggest that the ingested hydroids were being culled from the water column. The results of this study agreed with the assessments of Gallaway et al. (1981) and Randall and Hartman (1968) that sponges comprise a portion of the diet. Randall and Hartman (1968) also found that zoantharians, polychaetes, and tunicates were a portion of the stomach contents of Atlantic spadefish.

Although the *IRI* indicated that amphipods were highly important in stomachs obtained by nets and spearing, the numerical bias against the colonial and soft-bodied organisms made it difficult to determine the relative importance of prey of Atlantic spadefish with this index. For this reason, the *MI* was a more reliable measure of relative importance of food in stomachs of *C. faber*. If only soft-bodied and colonial prey were involved, the *IRI* would serve quite adequately; however, when noncountable and countable organisms occur in the same stomachs, numerical bias will make such an index less indicative of the relative importance of different prey. Although it is possible that Atlantic spadefish eat hydroids as a means of simplifying capture of epifaunal invertebrates (such as amphipods) that are usually associated with hydroids, the frequent occurrence of other cnidarians, such as sea anemones and sea pansies (which appeared to support fewer epifaunal invertebrates) in the diet, suggests otherwise.

The diet of *C. faber* collected by hook-and-line was quite different from that of fish obtained by nets and spearfishing. Hook-and-line sampling apparently created a biased overestimate of the importance of jellyfish in the diet of *C. faber*. Moore et al. (1984) used

the same hook-and-line method to capture Atlantic spadefish for stomach content analysis, and similarly found a preponderance of cannonball jellyfish in the diet. Spearfishing may have introduced some bias as well, since this method of collection concentrated on nearbottom fish that were closely associated with the artificial reefs. I observed that Atlantic spadefish spend some time higher in the water column, and schools were occasionally seen at the surface. Atlantic spadefish have also been observed eating *Stomolophus meleagris* and ctenophores at the surface in artificial reef areas (D.L. Hammond, SCWMRD, Charleston, SC 29412, pers. commun., May 1987). Although few ctenophores were identified in this study, their importance to the diet may have been underestimated since the mutilation of ctenophores by ingestive and digestive processes could have made them difficult to detect during analysis of stomach contents. Although jellyfish occurred in the stomach of only one Atlantic spadefish obtained by spearfishing and nets, it was possible that these organisms were more important in the diet than indicated. However, they appear to be considerably less important than indicated by hook-and-line collections.

The shift from a diet dominated by hydroids in strata 1 and 3 to a diet composed primarily of anthozoans in stratum 2 was probably a reflection of differences in food resources available in the different habitats. Juvenile Atlantic spadefish in estuaries (stratum 1) frequent wharves, pilings, and piers (Hildebrand and Schroeder 1928) where hydroids are a major part of the fouling community (Sutherland 1977). Hydroids are also a dominant component of fouling communities on offshore structures (stratum 3) (Wendt et al. 1989). Hydroids were probably less abundant in stratum 2 since unstable substrates, such as sand, generally support fewer hydroids (Calder 1976). However, sea pansies are typically located in sandy bottoms (Barnes 1980) and have been reported as a benthic component in South Carolina's sandy nearshore areas (Shealy et al. 1975, Van Dolah et al. 1983). A similarity in the diets of fish collected from strata 2 and 3 was the presence of an appreciable amount of terebellid polychaete tentacles. Perhaps polychaete tentacles and sea pansies presented a somewhat similar target to *C. faber* since both prey commonly feed with a mass of feeding structures extended from the sand; this suggested that a grazing-type feeding behavior was taking place along sandy bottoms.

Examination of the differences in diets among size classes of Atlantic spadefish showed all size classes relied heavily on hydroids. Although young-of-the-year fish in stratum 1 ate mainly hydroids and relied little on anthozoans for food, the high value for Anthozoa in the diets of small fish (<101 mm SL) was a reflection of numerous young-of-the-year fish which were collected from stratum 2 in increasing numbers beginning in the early fall. The high values for amphipods in fish 101–200 mm SL was primarily due to unusually large numbers (>1200 individuals in one stomach) found in three stomachs from a single collection at the Murrell's Inlet jetties; a large volume of hydroids was also present in these stomachs. Overall, major changes in food habits within the size range examined were not apparent; even the smallest fish examined (19 mm SL) had eaten primarily hydroids. Differences that existed probably reflected changes in habitat with increasing size. No information is currently available about food habits of larval *C. faber*.

Age and growth

Some information is available about early development of *C. faber* (Ryder 1887, Hildebrand and Cable 1938, Johnson 1978); however this study presents the only known information of this species' later growth with age. Although the location of the first annular mark on the otoliths has not been thoroughly validated, the size of fish with only one opaque zone on the sagittae corresponded well with the lengths of fish in the second group of a size-frequency distribution (Fig. 6). This also agreed with Hildebrand and Cable (1938), who believed Atlantic spadefish in North Carolina attained a length of 55–100 mm by the end of the first summer and a length of 135 mm (type of measurement unspecified; probably TL) during their second summer. Consequently, I am confident that the first opaque zone is the first annulus. Since young-of-the-year Atlantic spadefish are easily obtained from South Carolina estuaries during the summer and they can survive relatively well in captivity, more thorough validation of the first annulus, as well as additional yearly marks, may be obtained through daily growth studies and marking of otoliths with a chemical such as tetracycline (Beamish and McFarlane 1987).

Marginal increment analysis supported the hypothesis that the opaque zones on sagittae are annuli since they appeared to be formed once a year (over the winter months), although fish were available at collection sites only between May and December. In addition, the data showed (1) a strong relationship between otolith radius and length of the fish; (2) a decrease in growth rate in length with age (except where obscured by small sample sizes); and (3) close agreement between back-calculated lengths and observed lengths at age. The mean asymptotic TL ($L_\infty = 490$ mm TL) was reasonable for South Carolina's Atlantic spadefish population, but small for tropical regions where Atlantic spadefish with lengths up to 900 mm (presumably TL) have been reported (Breder 1948, Johnson 1978).

Reproduction

Few studies have dealt with the reproductive biology of *C. faber*. Hildebrand and Cable (1938) observed fully mature ripening females at around 135 mm, a size thought to have been attained during the second year (age 1); similarly, I found that all females age 1 and older were mature. Spawning of *C. faber* off South Carolina occurred May to October, and some females spawned more than once (serially) during this period. Serial spawning may allow fishes to produce a greater number of eggs than would be possible if they spawned only once during the year (DeMartini and Fountain 1981). The largest percentage of the fish were prepared to spawn in May, and histological evidence indicated that spawning continued periodically until August. Herrema et al. (1985) found Atlantic spadefish in spawning condition March through June along the east coast of Florida; however, few Atlantic spadefish were collected or examined. Chapman (1978) observed spawning aggregations of *C. faber* during late July off the coast of Georgia. No fecundity estimates for *C. faber* exist, but researchers investigating this would probably wish to use batch fecundity methods which utilize ova diameters to establish groups of eggs that will develop and be spawned at different times (DeMartini and Fountain 1981, Hunter et al. 1985).

The complete life history of the Atlantic spadefish is not well known and warrants further investigation. This study indicated that Atlantic spadefish in South Carolina waters spawn offshore late spring through early fall, with the juveniles subsequently moving into and inhabiting estuarine areas. In the fall, young-of-the-year Atlantic spadefish move into shallow offshore areas, which are also inhabited by age 1 individuals. Historical trawl data from SCWMRD indicated that *C. faber* juveniles were rarely taken in trawls off the coast of South Carolina during winter months, although they were taken in increasing numbers when proceeding southward toward Cape Canaveral, Florida (C.A. Wenner, Mar. Resour. Res. Inst., SCWMRD, Charleston, SC 29412, pers. commun., March 1987). In addition, analysis of trawl data from 1973 to 1980, by depth, showed that during the summer young (TLs corresponded to age 0 and age 1) Atlantic spadefish off the coasts of Georgia and Florida were located in depths of 20 m or less, while during the winter the majority of the catches were from depths of 28–56 m (G.R. Sedberry, Mar. Resour. Res. Inst., SCWMRD, Charleston, SC 29412, pers. commun., March 1987). This suggests that the age 0–age 1 group may move southward and into deeper water as the nearshore water cools. Age-2 and older Atlantic spadefish, which are common on South Carolina's artificial reefs and in high-relief live-bottom areas during the summer, are apparently rare in these areas during the winter.

Practically nothing is known of the whereabouts of South Carolina's Atlantic spadefish during the winter, although a commercial trawler reported capturing several thousand *C. faber* in a single trawl during the winter 50 km off South Carolina's coast (Ogle 1987). Perhaps the fish from artificial reef areas move into deeper water during the winter, returning to these structures the following spring as water temperatures increase along the coast.

Presently, there is an effort by SCWMRD personnel to promote tagging of Atlantic spadefish by recreational fishermen (D.L. Hammond, SCWMRD, Charleston, SC 29412, pers. commun., May 1987). Many more fish will probably have to be tagged before adequate returns are seen, but tagging could lead to an increased understanding of *C. faber* movements, allow population estimates to be made, and, if used in conjunction with tetracycline marking of otoliths, could lead to thorough validation of the ageing technique presented here.

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Appendix

Percent frequency of occurrence (%*F*), percent of total number (%*N*), percent of total volume (%*V*), index of relative importance (*IRI*), and the modified index of importance (*MI*) for food items of *Chaetodipterus faber* collected in South Carolina waters using nets or pole spears.

Prey item	%*F*	%*N*	%*V*	*IRI*	*MI*
Algae					
Cladophora laetiverens	0.65	0.03	0.01	0.03	0.01
Gracilaria folifera	3.23	0.14	1.25	4.49	4.04
Hypnea musciformis	3.87	0.17	0.82	3.83	3.17
Ulva sp.	0.65	0.03	0.03	0.04	0.02
Algae undetermined	8.39	0.37	0.12	4.08	1.01
Total Algae	12.90	0.73	2.33	39.56	30.06
Porifera					
Leucoselenia sp.	0.65	0.03	0.02	0.03	0.01
Scypha barbadiensis	0.65	0.03	0.50	0.34	0.33
Scypha sp.	0.65	0.03	0.42	0.29	0.27
Porifera undetermined	5.16	0.23	11.74	61.76	60.58
Total Porifera	6.45	0.31	13.25	87.50	85.46
Cnidaria					
Hydrozoa					
Aglaophenia rigida	0.65	0.03	0.07	0.06	0.05
Aglaophenia sp.	1.29	0.06	0.05	0.14	0.06
Campanularia sp.	0.65	0.03	0.01	0.03	0.01
Clytia sp.	1.29	0.06	0.04	0.12	0.05
Dynamena cornicina	0.65	0.03	0.22	0.16	0.14
Dynamena sp.	0.65	0.03	<0.01	0.02	<0.01
Eudendrium rameum	1.29	0.06	0.67	0.94	0.86
Eudendrium ramosum	3.87	0.17	1.98	8.31	7.66
Eudendrium sp.	21.94	0.96	12.55	296.39	275.35
Halocordyle disticha	3.23	0.14	0.38	1.67	1.23
Lafoea fruticosa	1.29	0.06	0.53	0.76	0.68
Lytocarpus sp.	1.29	0.06	0.02	0.10	0.03
Monostaechas quadridens	0.65	0.03	0.08	0.07	0.05
Obelia dichotoma	1.94	0.08	0.18	0.51	0.35
Obelia geniculata	1.94	0.08	0.41	0.95	0.80
Obelia sp.	3.87	0.17	0.72	3.46	2.79
Plumularia sp.	0.65	0.03	0.56	0.38	0.36
Sertularia distans	5.81	0.25	0.04	1.70	0.23
Sertularia sp.	3.23	0.14	0.07	0.68	0.23
Sertulariidae	2.58	0.11	1.69	4.66	4.36
Tubulariidae	0.65	0.03	0.22	0.16	0.14
Hydrozoa undetermined	43.87	1.92	4.91	299.29	215.40
Total Hydrozoa	79.35	4.51	26.53	2463.62	2105.16
Anthozoa					
Actiniaria	14.84	3.41	7.73	165.34	114.71
Octocorallia	0.65	0.03	0.50	0.34	0.33
Renilla reniformis	16.77	6.20	9.33	260.56	156.46
Total Anthozoa	29.03	9.64	18.35	812.54	532.70
Scyphozoa					
Chiropsalmus quadrumanus	0.65	0.03	9.37	6.06	6.09
Ctenophora	4.52	0.20	0.36	2.52	1.63
Annelida					
Polychaeta					
Sabellaria sp.	1.29	0.11	<0.01	0.15	<0.01
Sabellariidae	0.65	0.08	0.01	0.06	0.01
Terebellidae	12.90	0.56	22.72	300.39	293.09
Polychaeta undetermined	3.23	0.14	0.39	1.70	1.26
Total Polychaeta	17.42	0.90	24.14	436.17	420.52

Appendix (continued)

Prey item	%F	%N	%V	IRI	MI
Mollusca					
Gastropoda					
Anachis sp.	0.65	0.06	0.01	0.04	0.01
Mitrella lunata	0.65	0.03	0.01	0.02	0.01
Nudibranchia	0.65	0.11	0.01	0.08	0.01
Turbonilla sp.	0.65	0.03	<0.01	0.02	<0.01
Gastropoda undetermined	2.58	0.11	0.03	0.37	0.08
Total Gastropoda	5.16	0.34	0.06	2.03	0.31
Pelecypoda					
Anadara transversa	0.65	0.03	<0.01	0.02	<0.01
Musculus lateralis	4.52	0.31	0.02	1.47	0.09
Pelecypoda undetermined	5.16	0.42	0.14	2.89	0.72
Total Pelecypoda	9.68	0.76	0.16	8.91	1.55
Arthropoda					
Pycnogonida					
Anoplodactylus insignis	0.65	0.03	0.02	0.03	0.01
Crustacea					
Ostracoda	1.94	0.11	<0.01	0.22	<0.01
Copepoda					
Calanoida	1.29	0.08	<0.01	0.11	<0.01
Cyclopoida	1.29	0.37	<0.01	0.48	<0.01
Harpacticoida	9.68	3.35	0.03	32.76	0.29
Copepoda undetermined	0.65	0.17	<0.01	0.11	<0.01
Total Copepoda	12.26	3.98	0.04	49.17	0.49
Cirripedia					
Balanus sp.	5.16	0.37	0.07	2.24	0.36
Cirripedia undetermined	1.94	0.14	<0.01	0.28	<0.01
Total Cirripedia	7.10	0.51	0.07	4.13	0.50
Mysidacea	0.65	0.06	<0.01	0.04	<0.01
Tanaidacea	0.65	0.03	<0.01	0.02	<0.01
Isopoda					
Paracerceis caudata	0.65	0.17	0.02	0.12	0.01
Amphipoda					
Ampithoe sp.	5.16	1.30	0.06	7.00	0.31
Batea catherinensis	7.10	1.01	0.03	7.41	0.21
Caprella equilibra	11.61	3.07	0.15	37.44	1.74
Caprella penantis	17.42	42.46	2.25	778.74	39.20
Caprellidae undetermined	3.23	0.54	0.01	1.76	0.03
Cerapus tubularis	1.94	8.09	0.18	16.01	0.35
Dulichiella appendiculata	1.94	0.28	0.04	0.62	0.08
Erichthonius brasiliensis	18.71	6.06	0.22	117.50	4.12
Gammaridea undetermined	11.61	0.90	0.03	10.83	0.35
Gammaropsis sp.	2.58	0.23	0.01	0.60	0.03
Hyperiidae undetermined	0.65	0.03	<0.01	0.02	<0.01
Jassa falcata	7.74	8.91	0.31	71.39	2.40
Lembos sp.	1.29	0.14	<0.01	0.19	<0.01
Luconacia incerta	2.58	0.54	0.02	1.44	0.05
Phtisica marina	4.52	1.16	0.05	5.43	0.23
Stenothoe georgiana	5.16	1.10	0.03	5.83	0.15
Stenothoe minuta	3.23	0.23	0.01	0.74	0.03
Stenothoe sp.	0.65	0.03	<0.01	0.02	<0.01
Total Amphipoda	45.81	76.06	3.55	3646.63	162.63
Decapoda					
Natantia undetermined	1.29	0.11	0.05	0.21	0.06
Xanthidae undetermined	0.65	0.03	0.01	0.02	0.01
Brachyura undetermined	2.58	0.17	0.02	0.48	0.05
Decapoda undetermined	1.29	0.06	0.01	0.09	0.01
Total Decapoda	4.52	0.37	0.09	2.05	0.41

Appendix (continued)

Prey item	%F	%N	%V	IRI	MI
Bryozoa					
Anguinella palmata	1.94	0.08	0.02	0.19	0.04
Bugula neritina	7.74	0.34	0.15	3.75	1.16
Bugula sp.	1.29	0.06	0.01	0.09	0.01
Schizoporella errata	0.65	0.03	<0.01	0.02	0.01
Sundanella sibogae	1.29	0.06	0.07	0.16	0.09
Bryozoa undetermined	7.10	0.31	0.07	2.68	0.50
Total Bryozoa	17.42	0.87	0.33	20.92	5.75
Echinodermata					
Ophiuroidea undetermined	1.94	0.08	0.04	0.24	0.08
Chordata					
Urochordata					
Ascidiacea					
Didemnum candidum	0.65	0.03	<0.01	0.02	<0.01
Distaplia bermudiensis	1.29	0.06	0.07	0.16	0.09
Eudistoma carolinense	1.94	0.08	0.30	0.75	0.58
Ascidiacea undetermined	0.65	0.03	0.04	0.04	0.03
Total Ascidiacea	3.23	0.20	0.43	2.03	1.39
Pisces (scales)	0.65	0.03	<0.01	0.02	<0.01
Eggs undetermined	1.94	0.08	0.84	1.72	1.63

Number of stomachs examined: 177

Examined stomachs with food: 155

Abstract.—This study develops and demonstrates a framework for measuring changes in the total-factor productivity of fishing fleets operating in common-property, open-access fisheries. This approach is distinguished from previous efforts to measure productivity growth in fisheries by our explicit treatment of the fishery resource as a constraint on production and by the incorporation of recent advances in productivity measurement that take into account variations in the degree of capacity utilization in an industry. The approach is developed in sufficient detail for the non-economist fishery analyst to follow and implement. The empirical analysis of total-factor productivity growth in the U.S. tropical tuna fleet reveals that this approach eliminates a significant amount of bias in fleet productivity measures which is otherwise introduced when using traditional methods of productivity analysis.

On Measuring Fishing Fleet Productivity: Development and Demonstration of an Analytical Framework

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Measuring changes in productivity has long been an important component in evaluating an industry's economic performance. Such measures in fishing industries can signal the need for, as well as indicate the success of, policy or management actions. Measurement of productivity growth or technical progress in marine fishing industries has received attention by Bell and Kinoshita (1973), Davis et al. (1987), Duncan (n.d.), Kirkley (1984), and Norton et al. (1985).

Two considerations not addressed by previous researchers are important for evaluating productivity growth in fishing industries. First, traditional measures of productivity implicitly assume that a fishing industry's capital stock is being utilized, in an economic sense, at its long-run equilibrium or capacity output level. Thus, traditional measures fail to adjust for variations in the degree of utilization of the industry's productive capacity. Second, the effect of changes in abundance of the fish stock on productivity growth in fishing industries has not been specifically accounted for in the traditional analysis. As a result, changes in resource abundance are not disentangled from changes in productivity.

In this study we develop a nonparametric framework utilizing the method of growth accounting and economic index numbers to analyze the productivity growth of fishing fleets operating in common-property, open-access fisheries. The framework is then demonstrated by analyzing productivity growth in the U.S. tropical tuna purse seine fleet over the years 1981–1985.[1] We also demonstrate a method for deriving implicit aggregate output and input price indices for the purse seine fleet.

In developing the productivity assessment framework, we introduce further refinements to the standard procedure described by Denny et al. (1981) and Cowing et al. (1981)—which has seen continual improvement since the pioneering work of Solow (1957)—by adjusting for variations in capacity utilization and changes in resource abundance. The exposition includes the technical detail necessary to provide the non-economist fishery analyst with a comprehensible and useful means of tracking and analyzing productivity growth and performance in fisheries.

[1]The method is non-parametric because parameters of the production technology or production function are not econometrically estimated. The method of growth accounting and economic index numbers is discussed in a later section of the text. Econometric estimation of productivity growth does not impose the conditions of a constant-returns-to-scale production technology and Hicks-neutral technical change. However, this comes at the expense of more demanding data requirements: either a longer time-series of aggregate data or more vessel-level observations in any given year. In addition, some fairly sophisticated econometrics and economics are required to estimate and interpret the results.

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In the following section we introduce the methodology used to analyze total factor productivity in fishing fleets. The potential bias from failing to account for variation in economic capacity utilization is investigated in the third section. We discuss the data, empirical issues, and the construction of index numbers for the U.S. tropical tuna purse-seine fleet in the fourth section, and then we develop the implicit price indices and report and interpret results of the empirical analyses in the fifth section.

Total-factor productivity

The standard procedure for estimating total-factor productivity is derived from the economic theory of production. In common-property natural resource industries, the production function expresses a stock-flow relationship between the resource stock and the flow of resource extraction or output from the production activity in any given time-period. An important consideration when measuring productivity growth in fishing industries is defining the role of the common-property resource stock in the production technology.

Rather than treating the common-property resource as a conventional input (Scott 1954, Clark 1976, Dasgupta and Heal 1979), it is more appropriately specified as a constraint to the production technology. The fish stock is a biological constraint on the production technology because its abundance affects the production environment within which fishing firms operate, but it is beyond the control of any individual firm. That is, the use of conventional inputs such as capital, labor, and energy is conditional upon expected resource-abundance levels. Changes in resource abundance shift the production technology. McFadden (1978) develops this approach by treating environmental parameters (such as resource abundance) in a manner similar to disembodied technical change; i.e., technological progress due to more efficient use of existing inputs. Finally, resource abundance is a technological constraint because the total catch cannot exceed the abundance available, and an increase (decrease) in resource abundance allows an increase (decrease) in catch for any given level of input usage and state of technology.[2]

[2]Gordon (1954) similarly treated biological abundance as a technological constraint. Gordon (p. 136) states, "For each given level of population, a larger fishing effort will result in larger landings. Each population contour is, then, a production function for a given population level." Moreover, as Gordon noted, this approach does not preclude the impact that increases in catch typically have in reducing the resource stock. If resource abundance was instead another factor of production, like labor or capital, then changes in resource abundance would imply movements along the existing production function rather than shifts up or down the production function.

When the fish stock is treated as a technological constraint, the production function, F, relates the maximum flow of output in time t (such as tons of fish extracted), $Y(t)$, to the flow of $N+1$ inputs, $X_1(t)$, $X_2(t),\ldots,X_{N+1}$, the state of technology represented by $A(t)$,[3] and abundance of the fish stock indexed by $B(t)$:

$$Y(t) = F[X_1(t), X_2(t),\ldots,X_{N+1}(t); A(t), B(t)]. \quad (1)$$

Growth-accounting framework

Total-factor productivity measures are derived from equation (1) using the growth-accounting framework and economic index numbers.[4] This approach accounts for the growth in output flow over time by partitioning this output growth among the growth in inputs, technical progress, and changes in resource stock abundance. Total-factor productivity is then measured as the residual in the growth of output flow after accounting for all of the measurable sources of growth.

Under the growth-accounting framework, a constant-returns-to-scale production function is assumed, so that a proportional increase in inputs yields a proportional increase in output flow for any given level of resource stock abundance and state of technology. Movement in time t is assumed to lead to improvements in the state of technology, so that $\delta F/\delta A(t)>0$ (Solow 1957). Following conventional practice, we further assume a particular form of technological change, Hick's-neutral disembodied technical change.[5] Moreover, $\delta F/\delta B(t)>0$, so that increases (decreases) in resource stock-size allow an increase (decrease) in the flow rate of extraction for any given input bundle and state of technical progress. We assume a Schaefer (1957)-type production technology, and further assume that changes in resource stock-size are Hick's neutral, so that the

[3]The state of technology refers to the current level of technology or kind of production process utilized. For example, the current state of technology in the U.S. tuna fleet is represented by purse seining with some level of usage of vessel electronics.

[4]For a discussion of some of the limitations to the growth-accounting approach to measuring total-factor productivity, see Nelson (1981).

[5]Technological change or progress refers to the changes in a production process that come from the application of knowledge. These changes in the production process can be realized in various ways: through improved methods of utilizing existing resources, such that a higher catch-rate per unit of input ("effort") is obtained for a given level of resource stock abundance, often referred to as disembodied technological change; through changes in input quality, referred to as embodied technological change; or through the introduction of new processes and new inputs, which can be either (or both) disembodied and embodied technological change.

Hick's neutral technological change, whether disembodied or embodied, means that the technological advance does not change the proportions in which different inputs are used. Thus, for example, after technological change, capital, labor, energy, and any other inputs would be combined in the same proportions as before.

proportions with which all inputs are used remain constant for any given level of resource stock abundance.

The productivity growth-accounting measure is fully developed in the Appendix, while only its final form is presented here:

$$\frac{\dot{A}}{A} = \frac{\dot{Y}}{Y} - \sum_{i=1}^{N+1} S_i \frac{\dot{X}_i}{X_i} - \frac{\dot{B}}{B}, \qquad (2)$$

where the dots over variables represent time derivatives, $S_i(t) = P_i(t)X_i(t)/P(t)Y(t)$; i.e., the income or cost share of input X_i, where $P_i(t)$ is the price of input X_i in time t, and $P(t)$ is the price of output Y in time t. Productivity growth $\dot{A}/A$ is the residual of output growth $\dot{Y}/Y$ after accounting for aggregate input growth $\Sigma_i S_i(\dot{X}_i/X_i)$ and changes in resource abundance $\dot{B}/B$. This index of total-factor productivity growth is also called a Divisia index.

Tornqvist economic index numbers

A convenient discrete-time approximation to the continuous Divisia index is provided by Tornqvist (1936). The Tornqvist discrete approximation to the Divisia index of total-factor productivity growth (TFP) is expressed as:

$$\frac{TFP_t}{TFP_{t-1}} = \prod_{j=1}^{M} [Y_{jt}/Y_{j,t-1}]^{1/2(R_{jt}+R_{j,t-1})} - \prod_{i=1}^{N+1} [X_{it}/X_{i,t-1}]^{1/2(S_{it}+S_{i,t-1})} - \frac{B_t}{B_{t-1}}, \qquad (3)$$

where the Y_j are outputs, the X_i are the $N+1$ inputs, B is the index of resource abundance, the $R_j = P_jY_j/\Sigma_jP_jY_j$ are output revenue shares, and the S_i are $N+1$ input cost shares.[6] As the interval between time-periods approaches zero, discrete-time Equation (3) approaches continuous-time Equation (2).

[6]In practice, the logarithmic form of Equation (3) is computed, which gives the productivity growth between two periods. The exponent of this computation is then taken to obtain $TFP_{t,t-1}$. These period-to-period changes are then typically chained as in Equation (4) to form the Tornqvist bilateral chain index. The logarithmic form of the Tornqvist index is:

$$\ln(TFP_t/TFP_{t-1}) = 0.5 \sum_{j}^{M} (R_{jt} + R_{j,t-1}) \ln(Y_{jt}/Y_{j,t-1}) + 0.5 \sum_{i}^{N+1} (S_{it} + S_{i,t-1}) \ln(X_{it}/X_{i,t-1}) - \ln(B_t/B_{t-1}).$$

Chain indices

We use the method of chain indices to calculate the Tornqvist total-factor productivity index. Chain indices directly compare adjacent observations in a sequence of economic index numbers.[7] Nonadjacent observations are only indirectly compared, using the intervening observations as intermediaries, a practice resulting in transitive comparisons. The general form of the chain index can be written:

$$TFP_{t,t+N}^{\text{chain}} = TFP_{t,t+1} \cdot TFP_{t+1,t+2} \cdot \ldots \cdot TFP_{t+N-1,t+N}, \qquad (4)$$

where each individual term of Equation (4), $TFP_{t,t+1}$, is computed by the bilateral Tornqvist formula given in Equation (3), and represents the change from time period t to time-period $t+1$; i.e., $TFP_{t,t+1} = TFP_{t+1}/TFP_t$.

Productivity and capacity utilization

If firms are in long-run equilibrium, quasi-fixed inputs are optimally utilized in that the total cost of production per unit of output is minimized. This long-run optimal utilization is called full economic capacity utilization. Under long-run equilibrium, the flow of services from a quasi-fixed input is assumed proportional to the stock of that input, so that the available services from each of the quasi-fixed inputs are fully utilized: the observed stocks replace unobserved service flows in Equation (2) (Berndt and Fuss 1986).

When quasi-fixed inputs are not optimally utilized, i.e., the firm is not in long-run equilibrium, the observed productivity growth is composed of both the true technical progress impact, captured by $\dot{A}/A$ in Equation (2), and the rate of change in capacity utilization. An additional source of output variation is added to Equation (3): variations in capacity utilization (CU). To develop this argument, suppose that the $N+1^{th}$ input is now a quasi-fixed input capital (K), while the first N inputs are variable inputs. Then growth in productivity is written as (Hulten 1986):

$$\frac{\dot{A}}{A} = \frac{\dot{Y}}{Y} - \sum_{i=1}^{N} S_i \frac{\dot{X}_i}{X_i} - S_K \left[\frac{\dot{CU}}{CU} + \frac{\dot{K}}{K}\right] - \frac{\dot{B}}{B}, \qquad (5)$$

where S_K is capital's cost share.

[7]The alternative approach is that of fixed-base indices in which TFP in any time t is directly compared with TFP in the initial or base period. See Squires (1988) for an extensive discussion within fisheries.

Failure to capture this additional source of variation creates a potential bias in the true productivity residual, $\dot{A}/A$, which varies with the rate of capacity utilization.

Methods of capacity utilization adjustment

When the firm is in temporary or short-run equilibrium rather than long-run equilibrium, the productivity residual formula can be adjusted for variations in CU in two different ways. The first relaxes the assumption that service flows are proportional to stocks by adjusting the stock of a quasi-fixed input to reflect its flow of services[8] (Berndt and Fuss 1986). Thus, rather than specifying capital as a stock (e.g., the number of vessels in the fleet), capital is measured by its flow of services or total time of utilization (e.g., as fleet vessel-days fished). Such a flow adjustment corresponds to an economic notion of CU, because we assume that a producer's decision to increase or decrease running and fishing time is the outcome of an economic optimization process.

The second approach to adjusting the productivity residual for CU variations uses engineering notions of the proportion of available productive capacity that is actually being utilized. Let capacity output Y^* represent the maximum possible output level corresponding to "normal" input usage, existing technology, and the stocks of quasi-fixed inputs. A measure of capacity utilization is then obtained by the identity: $CU \equiv Y/Y^*$, where Y is the observed output level.

Data and empirical issues

Tornqvist output indices for the U.S. tropical tuna purse-seine fleet were constructed using annual deliveries of skipjack and yellowfin tuna by the fleet to U.S. canneries and the corresponding dollar values of these deliveries. Weighted exvessel implicit prices for skipjack and yellowfin tuna were calculated by dividing the total dollar value of cannery receipts for each species by the total volume of cannery receipts. Revenue and cannery receipts data were obtained from the Southwest Region, National Marine Fisheries Service (NMFS). Dollar values were deflated by the GNP implicit price index.

To construct the input indices, four major categories of factors used in owning and operating a tropical tuna purse seiner were identified: labor, capital, fuel, and other intermediate inputs (transshipment services, repairs, gear, insurance, helicopter services, travel, and other). Constant-dollar unit prices for these inputs were estimated based on purse-seine expenditure data reported by the U.S. International Trade Commission (ITC 1986).

The labor index incorporates the flow of labor services derived by multiplying estimated total days absent (at sea or absent from port) per vessel per year by 19 crew members, which is the assumed average crew size in each year of the period. The unit price of labor, cost per crew-day-absent, was estimated by dividing the sum of the ITC's reported annual crew-related expenditures per vessel by a measure of annual crew-days-absent per vessel.

Three different capital indices were constructed for the total-factor productivity analysis of the U.S. tropical tuna fleet. The first two capital indices both assumed that firms were in long-run equilibrium and that the flow of capital services was proportional to the capital stock. The first capital index specified capital as the annual number of vessels in the fleet. The second capital index captured the effect of different vessel sizes (where size is a measure of the vessel's hold or carrying capacity) upon catch rates by measuring capital as the annual carrying capacity of the fleet.

The third capital index not only captured the effects of different-sized vessels, but also accounted for actual changes in the flow of services from this size-differentiated capital stock. In this third case, the flow of capital services was measured in annual ton-days-absent, an aggregation of each vessel's carrying capacity multiplied by the number of days it spent at sea during the year. Measures of annual ton-days-absent were derived from purse-seine-fleet activity data compiled by NMFS. The cost share for capital used in construction of all the capital indices was its market rental price, the sum of the annual interest expense and reported annual depreciation per vessel from the ITC sample.

The fuel index was constructed by dividing the annual fuel expenditure per vessel (from the ITC sample) by average fuel prices provided by the American Tuna Boat Association. Fuel consumption per vessel was then multiplied by the number of vessels in the fleet resulting in the aggregate annual fuel consumption.

The index of other intermediate inputs was derived by deflating the fleet's nominal expenditure on this category of inputs by the producer price index for industrial commodities. This approach represents the collective use of these inputs in real terms. The nominal expenditure for this category of inputs divided by the corresponding deflated expenditure was used as a proxy for the unit price of other intermediate inputs.

[8] An alternative approach to accounting for variations in economic capacity utilization adjusts the cost or income shares rather than the flows of capital services. Berndt and Fuss (1986) and Hulten (1986) develop this approach, and Squires and Herrick (1988) provide a fisheries application. This approach is well suited when accurate and detailed data on running and fishing time are unavailable.

Table 1
Total-factor productivity growth in the U.S. tropical tuna fleet, 1981–85.

	No biomass adjustment				Biomass adjusted
	Capital input alternatives				
Period	No. of vessels[1]	Fleet carrying capacity[2]	Ton-days-absent[3]	Engineering-*CU*-adjusted carrying capacity[4]	Ton-days-absent; biomass adjustment[5]
1981–82	−0.1037	−0.1241	−0.0863	−0.1159	0.1006
1982–83	0.3739	0.3643	0.3378	0.1753	0.2120
1983–84	0.0298	0.0278	0.0767	0.1056	−0.4330
1984–85	0.0619	0.0499	0.0452	0.0932	0.0192
Mean	0.0905	0.0795	0.0933	0.0645	−0.0253

[1]Long-run equilibrium in capital, capital represented by the number of vessels; no biomass adjustment.
[2]Long-run equilibrium in capital, capital represented by fleet carrying capacity; no biomass adjustment.
[3]Capital input represented by the actual flow of capital services, ton-days-absent; no biomass adjustment.
[4]Capital represented by carrying capacity corrected for variations in capacity utilization (*CU*); no biomass adjustment.
[5]Capital represented by ton-days-absent; biomass adjusted.

Note: Calculated as Tornqvist bilateral indices using the logarithmic form of Equation (3) given in Footnote 6.

Because the U.S. tropical tuna purse-seine fleet operates almost exclusively in the Pacific Ocean, resource abundance measures relied on the extensive biological database that has been compiled by the Inter-American Tropical Tuna Commission (IATTC, La Jolla, CA 92038). From the IATTC database, we obtained estimates of annual yellowfin tuna biomass and estimates of catchability coefficients for yellowfin in the Commission's eastern tropical Pacific yellowfin regulatory area (CYRA). The CYRA was the only region of the Pacific for which such data were available. Moreover, there were no such data for skipjack tuna from any area of the Pacific. Because of these circumstances, it was not possible to explicitly account for fluctuations in biomass over the full range of the fishery and across all species harvested. Therefore, only the annual yellowfin biomass in the CYRA weighted by the catchability coefficient was used to adjust fleet productivity for changes in resource abundance.

Empirical results

Table 1 reports changes in annual total-factor productivity growth for the U.S. tropical tuna fleet over the period 1981–85 using Tornqvist bilateral-chain indices. Each of the total-factor productivity growth rates presented in Table 1 is distinguished by its specification of the capital input and adjustments for changes in resource abundance. Treatment of outputs and the other inputs is the same in all cases. To anticipate our results, we find that adjusting the traditional productivity measures for variations in economic capacity utilization and changes in resource abundance pares away sources of output growth that are not due to technical progress, giving a more accurate measure of productivity.

Productivity measures under full equilibrium

Columns (1) and (2) of Table 1 provide productivity growth measures assuming long-run equilibrium—economic capacity is fully utilized—without accounting for changes in resource abundance. The total factor productivity growth rates in column (1) use the first capital index: capital is represented by the number of vessels included in the fleet. The growth rates reported in column (2) are based on the second capital index: capital is represented by the carrying capacity of the fleet. Because vessels leaving the fleet during the period tended to be older and in the smaller size-categories, capital expressed in number of vessels decreased at a greater rate than capital measured in aggregate carrying capacity (columns [2] and [3] of Table 2). Hence, total-factor productivity growth based on the second capital index is lower than that based on the first capital index for those years in which the fleet declined.[9]

[9]It might be argued that technical progress is embodied in the capital stock, so that different ages of vessels, embodying different advances in technical progress, should be explicitly considered. This is referred to as vintage effects, and is certainly the case for some types of technical progress such as purse seining versus pole-and-line harvesting. However, in recent years, much of the technical progress has been in the form of vessel electronics. While this type of technological change in a narrow sense, represents embodied technical change, so that vintage effects could theoretically be important, the volume of investment is negligible in comparison with the vessel's value, and much of the technical change is fundamentally related to the managerial function, information, and learning-by-doing: Hick's-neutral technical change.

Table 2

Annual growth in output, capital, CYRA* yellowfin tuna biomass, and capital stock capacity utilization rates, 1981–85.

Period	Output[1]	No. of vessels[2]	Fleet carrying capacity[3]	Ton-days-absent[4]	CYRA yellowfin tuna biomass[5]	Rate of capacity utilization[6]
1981–82	−0.0090	0.0947	0.1151	0.0773	−0.1869	−0.0327
1982–83	0.1869	−0.1870	−0.1774	−0.1508	0.1258	0.3898
1983–84	−0.0165	0.0464	−0.0444	−0.0932	0.5096	−0.0244
1984–85	−0.0800	−0.1420	−0.1299	−0.1252	0.3167	−0.0125
Mean	0.0204	−0.0702	−0.0592	−0.0730	0.1913	0.0801

*Eastern tropical Pacific yellowfin regulatory area, IATTC.
[1]Annual change in deliveries of U.S.-caught yellowfin and skipjack tuna to U.S. canneries.
[2]Annual change in number of vessels comprising U.S. tropical tuna purse-seine fleet.
[3]Annual change in U.S. tropical tuna purse-seine fleet's hold capacity.
[4]Annual change in the fleetwide flow of capital services for the U.S. tropical tuna purse-seine fleet.
[5]Change in IATTC estimates of the annual CYRA yellowfin biomass.
[6]Annual change in ratio of actual U.S. tropical tuna purse-seine fleet output to fleet engineering capacity.

Note: In natural log form (cf. footnote 6).

Productivity measures adjusted for capacity utilization

The total-factor productivity growth rates presented in column (3) of Table 1 incorporate the third capital index: the annual flow of capital services from the size-differentiated capital stock, ton-days-absent. Since the number of ton-days-absent directly reflects the degree to which economic capacity is utilized, resulting measures of total-factor productivity growth are not subject to a capacity-utilization bias as are the growth rates shown in columns (1) and (2) of Table 1.

The effects of adjusting for *CU* are revealed in Table 2 by comparing the rates of change in the fleet's capital stock and the fleet's flow of capital services: fleet carrying capacity and ton-days-absent reported in columns (3) and (4), respectively. Between 1982 and 1983, fleet carrying capacity decreased 18%, while ton-days-absent decreased 15%. This means that the reduced fleet was fishing more intensively, and that a measure of productivity growth based on the stock of capital or fleet carrying capacity, without correcting for the degree of capacity utilization, will be biased upwards. Similarly, comparing growth in fleet carrying capacity and ton-days-absent between 1983 and 1984 reveals a greater decline in the latter relative to the former. Therefore, a smaller fleet capital stock is utilized (fished) proportionately less, and productivity growth based simply on the capital stock (carrying capacity) will be understated.

Column (4) of Table 1 reports growth in total factor productivity for the U.S. tropical tuna fleet, where changes in fleet carrying capacity—changes in the stock of capital—are corrected for variations in the rate of capacity-utilization. In this case, the capacity utilization adjustment is based on vessel design or engineering characteristics which act to establish an upper limit on fleet output in a physical sense. To estimate fleet engineering capacity, we assumed that each vessel was capable of making three fishing trips annually, filling its hold on each trip. Thus, maximum fleet output in each year is three times the fleet's carrying capacity. The ratio of actual fleet output (the total quantity of tuna delivered to canneries) to maximum potential fleet output estimates the degree of capacity utilization.

Changes in the rate of capacity utilization using the engineering adjustment are shown in column (6) of Table 2. These capacity-utilization rates were then used to derive the engineering-adjusted total-factor productivity growth rates presented in Table 1, column (4). Comparing the total-factor productivity growth rates in columns (2) and (4) of Table 1 discloses the extent of the bias introduced by failing to account for variations in the degree of capacity utilization.

The capacity-utilization adjustment is made to approximate the actual flow of services from the quasi-fixed factor, the capital stock. Therefore, one might expect the total-factor productivity growth rates using ton-days-absent (Table 1, column [3]) to closely correspond to those based on correcting for capacity utilization using the engineering approach (Table 1, column [4]). The fact that they do not points out that, in an economic sense, capacity-utilization adjustments explicitly recognize that quasi-fixed factors are not always utilized at the long-run equilibrium or full economic-capacity-output level, the level of output which minimizes the per-unit-cost of production. Under these circumstances, engineering-capacity output, as we have

Table 3
Implicit aggregate output and input price and total-factor-productivity chain indices.

Year	Total-factor productivity	Implicit aggregate output price	Implicit aggregate input price
1981	1.0000	1.0000	1.0000
1982	1.1058	0.9504	1.0221
1983	1.3669	0.8833	0.9016
1984	0.8865	0.7961	1.1941
1985	0.9037	0.7049	1.1099

Note: Implicit price indices formed by Fisher's weak factor-reversal relationship. See text for details. Total-factor productivity, calculated as Tornqvist bilaterial chain indices, adjusted for variations in biomass and capacity utilization (using ton-days-absent).

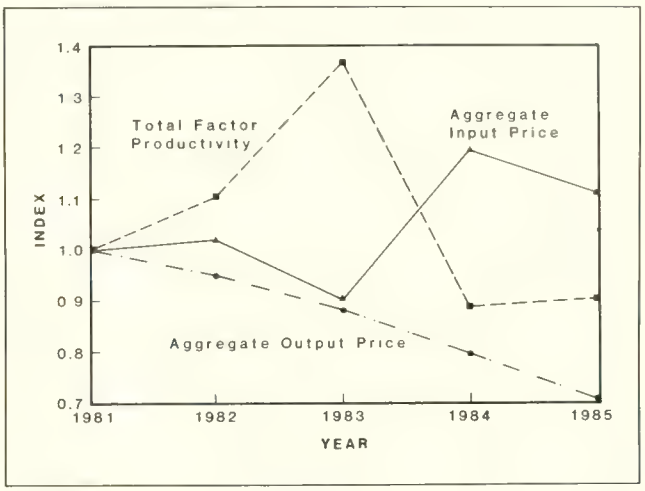

Figure 1
Total-factor productivity and implicit price indices.

defined it, should be greater than full economic-capacity output. Thus, the engineering capacity-utilization rates should be biased downward, and the corresponding productivity growth rates will inherit this bias. The preferred capacity-utilization correction, consistent with economic theory, should adjust the capital stock by its time in use to provide a flow measure of capital services.

Productivity measures adjusted for biological abundance

The total-factor productivity growth rates presented in column (5) of Table 1 are based on the actual flow of capital services and the growth of the yellowfin biomass in the CYRA (Table 2, column [5]). Comparing columns (3) and (5) of Table 1 indicates that the increase in the CYRA yellowfin biomass during most of the period acts to partially offset gains in total-factor productivity otherwise attributable to technical progress. The resource and capacity utilization adjusted total-factor productivity growth rates from Table 1, column (5) are used to compute the index of total factor productivity for the U.S. tropical tuna fleet shown in Table 3 and in Figure 1.[10]

Implicit output and input price indices

Fleet economic performance depends upon the real prices of outputs and inputs in addition to total-factor productivity. Corresponding to the aggregate output and input quantity indices are implicit aggregate output and input prices. These are calculated by a relationship due to Fisher (1922), which states that the product of the price index times the quantity index equals the expenditure ratio between the two time-periods. The implicit price index for an output (or input) can be interpreted as the ratio of the price level in period $t+1$ to the price level t. Fisher's relationship for the price (PI) and quantity (QI) indices for aggregate output Y can be written as:

$$PI(P_t, P_{t+1}, Y_t, Y_{t+1})\ QI(P_t, P_{t+1}, Y_t, Y_{t+1}) = \sum_i P_{it+1} Y_{it+1} / \sum_i P_{it} Y_{it}. \quad (6)$$

Given either a price index or quantity index, the other function can be defined implicitly by Equation (6).

Implicit Tornqvist bilateral-aggregate output-price and input-price chain indices for the U.S. tropical tuna purse-seine fleet, along with the resource-abundance adjusted total-factor productivity index, are presented in Table 3 and in Figure 1. Increases in total-factor productivity or output prices, or both, improve the fleet's economic performance, while increases in input prices worsen the fleet's economic performance.

Taken together, the changes in total-factor productivity, aggregate input-price, and aggregate output-price indices shown in Figure 1 and Table 3 indicate that the 1981–85 period was highly unstable with regard to the fleet's economic performance. Herrick and Koplin (1986, 1987) point out that this was a time of massive restructuring in the U.S. tuna industry, during which the U.S. fleet began a significant shift of its operations from the eastern to the western Pacific

[10]These period-to-period changes in total-factor productivity, i.e., productivity growth, were computed following footnote 6. Next, the exponent is taken of each value in column (5) of Table 1, giving $TFP_{t,t-1}$. The Tornqvist bilateral-chain index is then formed following Equation (4), to give the first column of Table 3. Note that the value 1.000 for 1981 is the exponent of zero, where zero refers to the zero change for the first period.

Ocean, and the U.S. canned tuna market was inundated by imports. These events undoubtedly contributed to the unstable pattern of productivity growth, and would have introduced additional, unmeasurable disturbance into the system which we are unable to disentangle from the productivity residual in the growth-accounting framework.[11]

Concluding remarks

We have shown how the nonparametric growth-accounting framework can be modified to measure the growth in total-factor productivity or technical progress of fishing fleets. This framework can provide useful information for tracking and analyzing economic growth and its causal factors in a fishing industry, particularly where short time-series of aggregate data are all that is available. Our approach can be readily implemented in fishing industries in both developed and developing countries, even by non-economist fishery analysts. Unique to our approach is the treatment of the fishery resource, not as a conventional input, but as a technological constraint on production. Our empirical analysis of total-factor productivity growth in the U.S. tropical tuna fleet demonstrates that disentangling the productivity residual from changes in resource abundance provides markedly different results.

We consider capital the most important component of aggregate input because it is represented by the basic unit of production, the fishing vessel. The capital stock—the fishing fleet—determines capacity output in both an economic and engineering sense. Theoretically, it is the flow of services from the capital stock that should serve as the capital input when measuring total-factor productivity. In practice, however, one may not have measures of the flow of capital services, in which case proper specification of the capital input, and accounting for temporary equilibrium effects such as variations in the degree of capacity utilization, becomes extremely important.

[11]Because our biomass adjustment is based only on changes in yellowfin tuna resource abundance in the CYRA, the variation in total-factor productivity should become more pronounced as the fleet moved from the eastern to the western Pacific Ocean during the 1981–85 period. Furthermore, there were likely to have been some initial technical inefficiencies as the fleet began fishing in the relatively unfamiliar western Pacific.

New investment and industry restructurings can have very real detrimental effects upon the time-path of productivity growth. Therefore, we would expect to see unstable productivity growth as firms adapt over time to changing industrial conditions. Under such circumstances, the assumptions underlying our model—constant-returns-to-scale, disembodied Hick's-neutral technical change conditions, and technical efficiency—may not fully apply. Nonetheless, these are limitations of virtually any application using the growth-accounting framework.

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Appendix

The growth-accounting framework is developed by differentiating Equation (1) with respect to time t:

$$\frac{dY(t)}{dt} = \sum_{i=1}^{N+1} \frac{\delta F}{\delta X_i(t)} \cdot \frac{dX_i(t)}{dt} + \frac{\delta F}{\delta A(t)} \cdot \frac{dA(t)}{dt} + \frac{\delta F}{\delta B(t)} \cdot \frac{dB(t)}{dt}, \tag{A.1}$$

where $dY(t)/dt$ represents the growth rate of output (i.e., extraction rate) due to technical progress. Putting the left side of Equation (A.1) into percentage terms (and suppressing the notation for each time period t) gives:

$$\frac{dY}{dt}\frac{1}{Y} = \frac{1}{F} \sum_{i=1}^{N+1} \frac{\delta F}{\delta X_i}\frac{dX_i}{dt} + \frac{\delta F}{\delta A}\frac{dA}{dt} + \frac{\delta F}{\delta B}\frac{dB}{dt}. \tag{A.2}$$

To obtain proportionate growth rates for all variables, substitute $[dY/dt][1/Y] = \dot{Y}/Y$, $[dX_i/dt][1/X_i] = \dot{X}_i/X_i$, $[dA/dt][1/A] = \dot{A}/A$, and $[dB/dt][1/B] = \dot{B}/B$ into Equation (A.2) to give:

$$\frac{\dot{Y}}{Y} = \sum_{i=1}^{N+1} \frac{\delta F}{\delta X_i}\frac{X_i}{F}\frac{\dot{X}_i}{X_i} + \frac{\delta F}{\delta A}\frac{A}{F}\frac{\dot{A}}{A} + \frac{\delta F}{\delta B}\frac{B}{F}\frac{\dot{B}}{B}. \tag{A.3}$$

In equation (A.3), by convention (Denny et al. 1981, Solow 1957) the term $[\delta F/\delta A][A/F]$ is the proportional shift in the production function with time and is set equal to unity. Thus a 1% increase in the index of technical progress increases the flow rate of output by 1%. This shifting of the production function through time is called technical change or the time rate of growth of technical progress. The term $[\delta F/\delta B][B/F]$ is set to unity because it is a technology-shift parameter for a Schaefer (1957)-type production technology in which catch rates are proportional to resource abundance for any given vector of inputs.[12]

Define $E_i = [\delta F/\delta X_i][X_i/F]$. This is the output elasticity of input X_i, representing the proportional change in output flow for a given change in X_i within some level of resource stock abundance and state of technological progress. Substituting the output elasticity expression into (A.3) gives the long-run rate of output growth as:

$$\frac{\dot{Y}}{Y} = \sum_{i=1}^{N+1} E_i \frac{\dot{X}_i}{X_i} + \frac{\dot{A}}{A} + \frac{\dot{B}}{B}, \tag{A.4}$$

[12]This corresponds to the production function specified by Schaefer (1957), $Y = F(E,B) = qEB$, where q denotes the catchability coefficient and E represents effort or an aggregate input index so that $E = g(X_1, \ldots, X_{N+1})$, where g is a linearly homogeneous aggregator function and the $N+1$ X_i are the inputs. Thus, $\delta Y/\delta B = 1$. We are grateful to Jim Kirkley who pointed this out to us. Moreover, the Schaefer production function implicitly assumes constant-returns-to-scale in inputs, because $\delta Y/\delta E = 1$, so that a proportionate increase in E generates an equal proportionate increase in Y. In addition, changes in the resource stock affect the production function in a Hick's-neutral manner, similar to technical progress.

or after rearranging:

$$\frac{\dot{A}}{A} = \frac{\dot{Y}}{Y} - \sum_{i=1}^{N+1} E_i \frac{\dot{X}_i}{X_i} - \frac{\dot{B}}{B}, \qquad \text{(A.5)}$$

where the dots over the variables represent time derivatives.

Equation (A.5) is the fundamental equation of growth accounting in its continuous time form. Thus full, long-run equilibrium total-factor productivity growth, $\dot{A}/A$, identified with technical progress, is a residual after the sources of output growth have been allocated among intertemporal changes in inputs and resource abundance for a constant-returns-to-scale production technology.

Equation (A.5) allocates the growth rate of $Y(t)$ among $A(t)$, $X(t)$, and $B(t)$ as required, but because the E_i are not observable, two additional steps are required for empirical analysis. Assuming that all inputs are paid the value of their marginal product, then $\delta F/\delta X_i(t) = P_i(t)/P(t)$, where $P(t)$ and $P_i(t)$ are the full equilibrium prices of output and inputs, respectively. This implies that: $S_i(t) = E_i(t) = P_i(t)X_i(t)/P(t)Y(t)$, where $S_i(t)$ is the income or cost share of input X_i. Under constant returns to scale, total costs equal total revenue; i.e., $\Sigma_i P_i(t)X_i(t) = P(t)Y(t)$, and $\Sigma_i S_i(t) = 1$.

The final step is to substitute $E_i(t) = S_i(t)$ into equation (A.5), which gives an equation in which all variables are measurable except $\dot{A}/A$, which is calculated as a residual:

$$\frac{\dot{A}}{A} = \frac{\dot{Y}}{Y} - \sum_{i=1}^{N+1} S_i \frac{\dot{X}_i}{X_i} - \frac{\dot{B}}{B}, \qquad \text{(A.6)}$$

where the notation for time-period t is again suppressed and $\Sigma_i S_i(\dot{X}_i/X_i)$ represents aggregate input growth. Productivity growth equals the rate of change of output flow minus a share-weighted index of rates of change of inputs minus the rate of change of the resource stock. The index of productivity growth in Equation (A.6) is also called a Divisia index (Hulten 1974).

Phylogeny and Biogeography of Hakes (*Merluccius*; Teleostei): A Cladistic Analysis

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Abstract.—The phylogeny and historical biogeography of hakes (*Merluccius*) are reexamined using a cladistic analysis of Inada's (1981) osteological data. One of the 188 most parsimonious trees (cladograms), which also has the lowest (best) *F* value, is congruent with the scheme of evolution proposed by Ho (1974) for the hake-specific copepod parasites. Offshore hake *M. albidus* is the sister group of all other extant hakes. Silver hake *M. bilinearis* is the sister group of the three eastern Pacific hakes: Chilean hake *M. gayi*, Panamanian hake *M. angustimanus*, and Pacific hake *M. productus*. The five Eastern Atlantic species, European hake *M. merluccius*, Senegalese hake *M. senegalensis*, Benguelan hake *M. polli*, shallow-water cape hake *M. capensis*, and deep-water cape hake *M. paradoxus*, are monophyletic and constitute the sister group that forms a trichotomy with Argentine hake *M. hubbsi* and New Zealand hake *M. australis*. The biogeography inferred from the most parsimonious phylogenetic hypothesis of hakes differs from the views given by both Inada (1981) and Kabata and Ho (1981). The ancestral hake in the eastern seaboard of North America diverged into two stocks. Subsequently, one of them vicariated into a northern and a southern population. The southern population moved southward first and then separated into three stocks, with one of them moving eastward and crossing the Atlantic in the region of low latitudes. One of the two remaining stocks moved further southward and entered the Pacific through the Drake Passage. After further divergence, a descendant stock of the northern population off the coast of North America also moved southward; it did not enter the south Atlantic, but, instead, moved into the Pacific over the submerged Panamanian Isthmus. Some geologic events are discussed for their possible effects in the formation of the present pattern of hake distribution.

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In 1981, two views on the historical biogeography of hake were proposed: one by T. Inada and the other jointly by Z. Kabata and J.S. Ho. Although inferred from different sets of biological information, ichthyological vs. parasitological, the two views are remarkably alike in most major points. Both views (Fig. 1) suggest that the hakes originated in the eastern North Atlantic and dispersed southward via two routes: one along the west coast of Europe and the other along the east coast of North America. These authors also arrived at the same conclusion that hakes entered the Pacific over the submerged Panamanian Isthmus. The major discrepancy between the two views lies in their accounts of the origin and dispersal of Argentine hake *Merluccius hubbsi*.

Using the coevolutionary relationships between hakes and their copepod parasites, Kabata and Ho (1981) suggested that the Argentine hake was derived from the western North Atlantic stock because it shares the subspecies of copepod parasite *Neobrachiella insidiosa lageniformes* with the silver hake *M. bilinearis* occurring off the east coast of North America. However, in contrast, Inada (1981) proposed that the Argentine hake was derived from an eastern South Pacific stock that rounded Cape Horn to reach Argentina. The Pacific origin of Argentine hake was first proposed by Szidat (1955, 1961), but Ho (1974) questioned its validity based on his studies on the copepod parasites of European hake *M. merluccius*, silver hake *M. bilinearis*, Chilean hake *M. gayi*, and shallow-water cape hake *M. capensis*. Contrary to the conclusion of Kabata and Ho (1981), Ho (1974) speculated that hakes originated in the western North Atlantic.

Recently, Fernandez (1985) studied the parasites of a population of New Zealand hake occurring at Guafo Island, Chile (lat. 43°36′S, long. 74°43′W), and corroborated the view of Kabata and Ho on hake biogeography. Since her study methods are the same as that of Kabata and Ho (1981), the above-mentioned disagreement between ichthyologist and parasitologist on the origin and dispersal of Argentine hake remains unresolved. A third method of investigation is needed.

Cladistic analysis is a systematic method that attempts to discover genealogical (phylogenetic) relationships of taxa (Hennig 1966, Wiley 1981). Since a detailed phylogenetic hypothesis for a group of organisms can and should serve as a basis for inferring the biogeographic history (Hennig 1966, Brundin 1966, Nelson and Platnick 1981, Humphries and Parenti 1986), I have used this approach to reexamine the phylogenetic relationships and biogeography of hakes. This paper reports my results.

Character analysis

In his revision of *Merluccius* Rafinesque, Inada (1981) recognized 12 species of hake (Table 1) and provided detailed redescription of each species, including measurements of 28

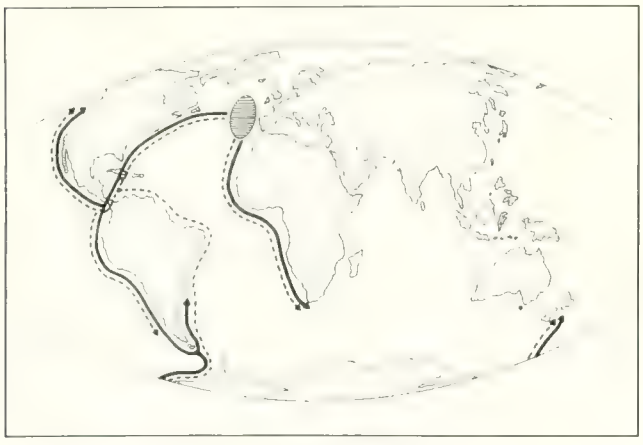

Figure 1
Distribution and movements of hakes as proposed by Inada (1981) (→) and Kabata and Ho (1981) (- - →).

Table 1
Extant species of hakes (*Merluccius*) recognized by Inada (1981), and their distribution.

Species	Common name	Distribution
merluccius	European hake	Europe, western North Africa
senegalensis	Senegalese hake	Western north Africa
polli	Benguelan hake	Mauritania to Angola
capensis	shallow-water hake	Angola to South Africa
paradoxus	deep-water cape hake	Nambia, South Africa
bilinearis	silver hake	Atlantic coast of North America
albidus	offshore hake	Western Atlantic, Gulf of Mexico, Caribbean
productus	Pacific hake	Pacific coast of North America
angustimanus	Panamanian hake	Baja California to Columbia
gayi	Chilean hake	Peru, northern Chile
hubbsi	Argentine hake	Argentina
australis	New Zealand hake	Southern Argentina, southern Chile, New Zealand

body parts and counts for nine meristic characters. Moreover, he added osteological information for 14 groups of bones, and discussed the distribution, biology, and fishery of all the species recognized. It is the most complete revision ever published on the genus *Merluccius*.

The morphological differences and diagnostic characters of the 12 species of hake were succinctly listed by Inada (1981, tables 37 and 38). Because quantitative variables are difficult to analyze cladistically (Pimentel and Riggins 1987), data in table 37 of Inada (1981) were not included in the present analysis. Thus, only the osteological information summarized in his table 38 was used.

Steindachneria is a problematical gadiform genus that has been treated as a merluciid or as a monotypic family with uncertain affinities. Recently, Fahay (1989) presented evidence from ontogenetic and osteological grounds to support the removal of the genus from the Merlucciidae. Nevertheless, in his report on the systematics of Merlucciidae, Inada (1989) concluded that the family contains four genera in two subfamilies, Steindachneriinae (*Steindachneria*) and Merlucciinae (*Lyconus*, *Macruronus*, *Merluccius*). This treatment is in line with Nolf and Steurbaut's (1989) result based on analysis of otolith features. Therefore, I included *Steindachneria* in my analysis of outgroup genera to determine the sister group of *Merluccius*.

The osteological information given in Inada's (1989) Table 1 was used in my search for outgroup genera. Lotinae was selected as the outgroup to polarize the character states of the four merlucciid genera, because both the works of Dunn (1989) and Nolf and Steurbaut (1989) indicate that it is the nearest sister group of Merlucciidae. Since six of the thirteen enumerated characters in table 1 of Inada (1989: 199) show no differences in their states among the five genera under consideration, they were excluded from the present analysis. The BRANCH AND BOUND algorithm from the phylogenetic computer package PAUP (version 2.4.1, David L. Swofford, Ill. State Nat. Hist. Surv., Urbana 61820), which guarantees the finding of all the most parsimonious trees, was used in this analysis. Two trees were obtained, both with a consistency index of 0.667. The one with the lower F value (= 0.174) is selected and reproduced in Figure 2. Unexpectedly, it shows that *Merluccius* is a sister group of the rest of the merlucciid genera. This disagrees with the phylogeny proposed by Inada (1989) and Okamura (1989).

According to the outgroup procedure as proposed by Maddison et al. (1984), all three genera—*Steindachneira*, *Macrouronus*, and *Lyconus*—were included in the analysis of the "outgroup node" for polarization of character states of the hake. Dr. Tadashi Inada (Tohoku Reg. Fish. Res. Lab., Same, Hachinohe 031, Japan, pers. commun., Dec. 1988) has kindly provided osteological information for these three genera. Appendix 1 gives the coding of osteological characters (Inada 1981) for the hake species, and Appendix 2 shows the matrix of the character states in the twelve extant species of hakes. A new species of hake, *Merluccius hernandezi*, has been reported from the Gulf of California (Mathews 1985) since revision of Inada. However, it is not included in the present analysis due to the lack of osteological information.

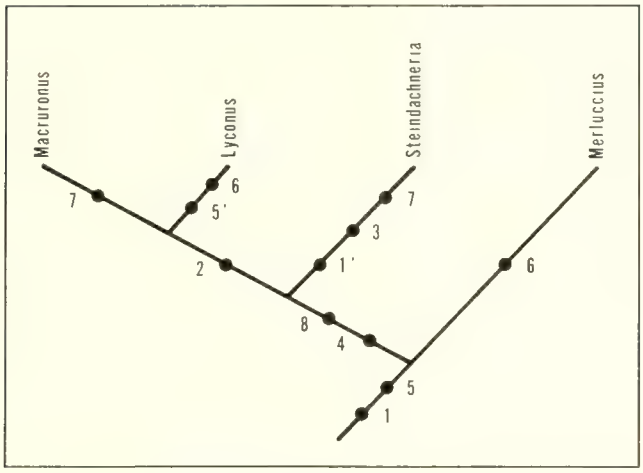

Figure 2

Cladogram showing hypothesized relationships of the merlucciid genera. Character codes: 1 = V-shaped crest on skull present; 1′ = V-shaped crest on skull absent; 2 = foramen for trigemino-fascialis nerve present; 3 = shape of anterior parasphenoid vertical; 4 = upper window on suspensorium closed; 5 = two dorsal fins; 5′ = one dorsal fin; 6 = one pseudospine in dorsal fin; 7 = two pseudospines in dorsal fin; 8 = caudal fin tapering.

Phylogeny

An unusually large number of trees (cladograms) were obtained, 188 in total, all with a consistency index of 0.522. The F value of these most parsimonious trees ranges from 0.277 to 0.482. However, there is only one tree with the lowest (best) F value, reproduced in Figure 3. Since the development of host specificity in parasites is the result of coevolution between the host and its parasite, an hypothesis of the host phylogeny should also apply to the phylogeny of its specific parasite. In other words, host-specific parasites can be useful to corroborate host phylogeny.

Brooks et al. (1986) suggested that the lower the F-ratio (= F value), the greater is the degree of historical constraint on the data. In this regard, the tree with the lowest F value (Fig. 3) should exhibit the highest degree of congruence with the parasite data set. To check this congruency, a parasite summary cladogram needs to be constructed. Figure 4 is such a cladogram, generated by replacing the hake species on the cladogram with each of their respective subspecies of *Neobrachiella insidiosa*, a host-specific copepod parasite of hakes. Since *Chondracanthus palpifer* Wilson was recently found by Villalba and Fernandez (1985) to parasitize not only *Merluccius* but also another merlucciid (*Macruronus magellanicus* Lönnberg) in Chilean waters, it can no longer be treated as a *Merluccius*-specific parasite as previously proposed. Accordingly, only the three subspecies of *Neobrachiella insidiosa* are considered.

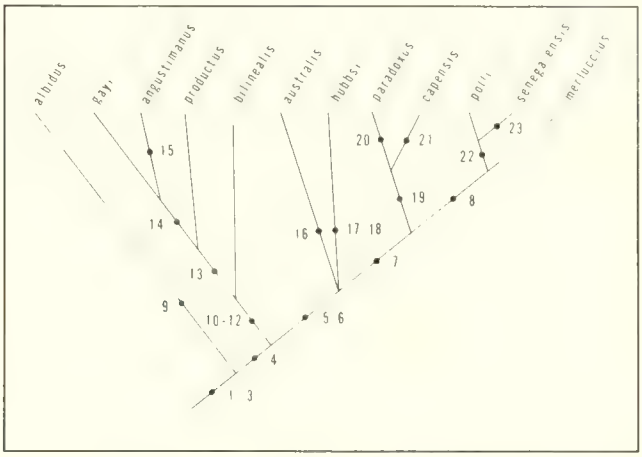

Figure 3

Cladogram showing hypothesized relationships among species of *Merluccius*. For character codes 1–23, see Appendix 1.

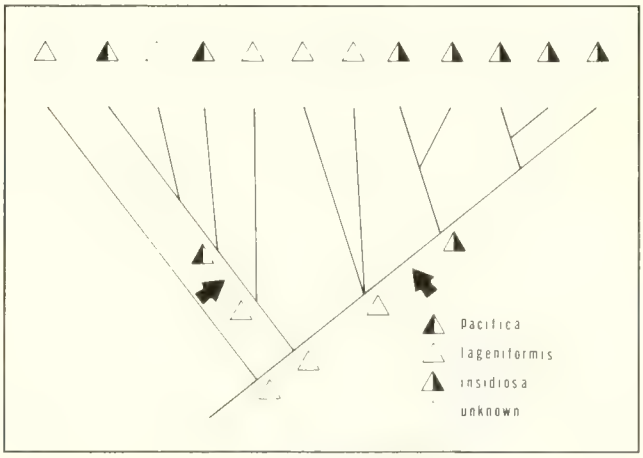

Figure 4

Parasite summary cladogram showing relationships among subspecies of *Neobrachiella insidiosa* inferred from hypothesized relationships among species of hake (*Merluccius*). Arrows indicate the changes (evolution) of parasites.

As in Figure 4, the result agrees, indicating that the hake-specific *Neobrachiella insidiosa* had changed (evolved) from *N. insidiosa lageniformes* (western Atlantic form) to *N. insidiosa insidiosa* (eastern Atlantic form) on one hand, and from the western Atlantic form (original form) to *N. indisiosa pacifica* (Pacific form) on the other. This scheme of evolution for *Neobrachiella insidiosa* contradicts the one proposed by Kabata and Ho (1981) but, nevertheless, agrees with the hake-parasite evolution proposed by Ho (1974). The phylogenetic hypothesis predicts a Pacific form of *N. insidiosa*, but it is yet to be found in *M. angustimanus*. The discovery of *N. insidiosa pacifica* on the Panamanian hake would strongly support the cladogram shown in Figure 3.

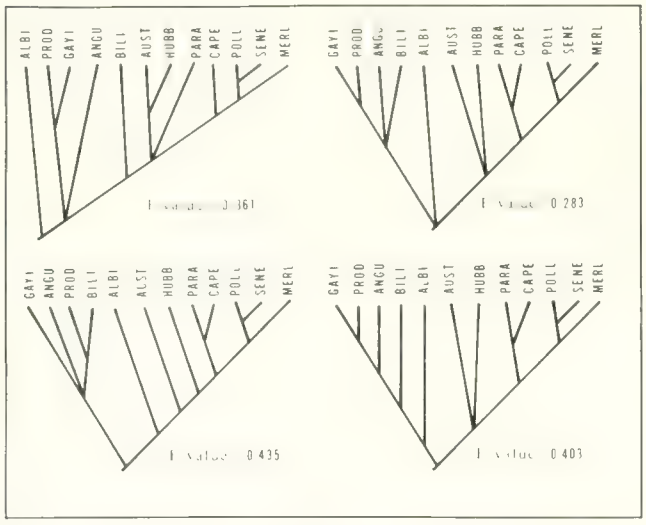

Figure 5

Examples of some most parsimonious cladograms of hakes (*Merluccius*). All have 23 steps and a consistency index of 0.522. Abbreviation of species names: ALBI = *albidus*; ANGU = *angustimanus*; AUST = *australis*; BILI = *bilinearis*; CAPE = *capensis*; HUBB = *hubbsi*; MERL = *merluccius*; PARA = *paradoxus*; POLL = *polli*; PROD = *productus*; SENE = *senegalensis*.

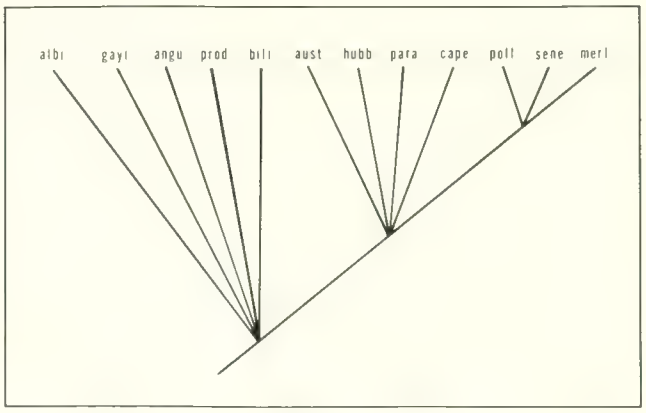

Figure 6

Strict consensus tree of hakes showing information common to the 188 equally parsimonious trees. For abbreviation of species names, see Figure 5.

With currently available information, the tree in Figure 3 is considered to be the better hypothesis than the other existing hypotheses of hake phylogeny. Admittedly, it has a high ratio of homoplasy (17/23 or 73.9%). Such frequent homoplasy is somewhat undesirable in a cladistic analysis. Nevertheless, using different sets of characters (number of gill-rakers, vertebrae, and fin rays), Inada (1981) identified five groups in his key to the species of *Merluccius*, with four species (*australis*, *bilinearis*, *hubbsi*, *polli*) in two groups, two species (*gayi*, *senegalensis*) in three groups, and one species (*capensis*) in four groups. This repeated sharing of many characters (high frequency of homoplasy) seems to be the norm in *Merluccius*.

Close examination of each of the 188 most parsimonious trees revealed that European hake *M. merluccius*, Senegalese hake *M. senegalensis*, Benguelan hake *M. polli*, shallow-water cape hake *M. capensis*, deep-water cape hake *M. paradoxus*, Argentine hake *M. hubbsi*, and New Zealand hake *M. australis* are always included in a monophyletic group. However, relationships among the three eastern Pacific hakes—Chilean hake *M. gayi*, Panamanian hake *M. angustimanus*, and Pacific hake *M. productus*—and the two western North Atlantic species—silver hake *M. bilinearis* and offshore hake *M. albidus* are not as consistent. Some representative trees are reproduced in Figure 5 for comparison. Offshore hake (ALBI, Fig. 5) appears to occupy the most plesiomorphic node in almost all cases. This is an indication that offshore hake is the extant species closest to the ancestral form.

The strict consensus tree in Figure 6 was obtained using the CONTREE algorithm contained in the PAUP program. It summarizes the point of agreement in all 188 equally parsimonious trees. Remarkably, the monophyletic relationships of the seven species of hakes occurring off the coasts of Europe, Africa, and eastern South America are also supported by this consensus tree.

Biogeography

According to the principle of vicariance biogeography (Nelson and Platnick 1981, Humphries and Parenti 1986), the pattern of spatial distribution attained by the hakes can be deduced from the phylogenetic hypothesis. The area summary cladogram in Figure 7 illustrates how the present pattern of hake distribution was attained. According to the progression rule of Hennig (1966), it implies that the ancestral hake, residing in the western North Atlantic, diverged into two lineages. One gave rise to the modern offshore hake (ALBI, Fig. 7), and the other formed the species A, which is the ancestor of all the remaining extant hake species. Species A vicariated into two populations: the northern population (C, Fig. 7) whose descendants later occupied the Pacific Ocean, and the southern population (B, Fig. 7), whose descendants gave rise to all the hakes in the western South Atlantic and entire eastern Atlantic.

I interpret the cladogram to mean that (1) hake originated in the western North Atlantic, (2) migrated southward and then eastward in the Atlantic, and (3) entered the Pacific in two ways, over the submerged

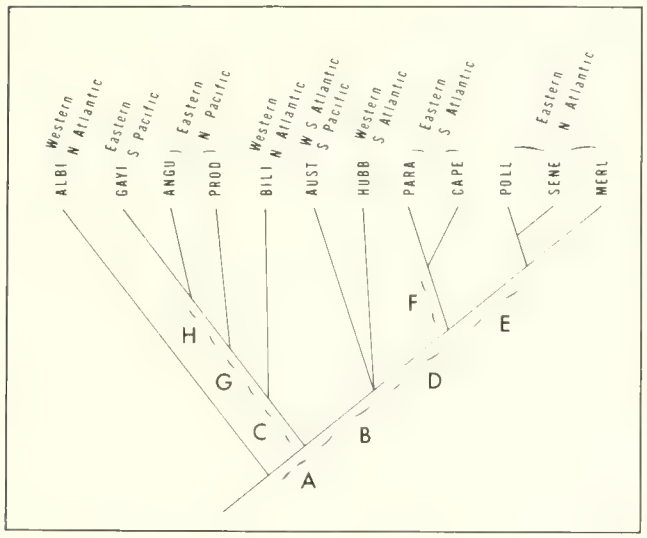

Figure 7
Area summary cladogram of hakes (*Merluccius*) with ancestral species (A–H). For abbreviation of species names see Figure 5.

Panamanian Isthmus and through the Drake Passage. Assertion (1) agrees with the proposal of Ho (1974) concluded from a work on host-specific copepod parasites of hake, but it contradicts Inada (1981) and Kabata and Ho (1981) who suggested otherwise. Assertion (3) is roughly the same as those suggested by Inada (1981) and Kabata and Ho (1981), differing only in the details. However, the 2nd assertion is a new discovery; this track has never been proposed.

Inada (1981) speculated that hakes had migrated out of the western Atlantic only once, when they dispersed to the southern hemisphere during the Pliocene over the submerged Panamanian Isthmus. He believed that the hakes could not have migrated to the South Atlantic along the coast of Brazil because the low salinity in the estuarine area of the Amazon River would have acted as a natural barrier to their dispersal. However, the Amazon River estuary was not an effective deterrent to hake dispersal in the early Tertiary. In work on the coevolution between freshwater stingrays and helminth parasites, Brooks et al. (1981) concluded that the Amazon Basin became a separate eastward-flowing entity in the Miocene. Moreover, Damuth and Kumar (1975) reported that the Brazilian plate developed a geosyncline downfold when the Andes began to fold up in the Pliocene, and, as the result of this lowering of the eastern side of the plate, the water from the landlocked sea (of the Pre-Amazonas) started to flow eastwards to the Atlantic. Therefore, during and prior to the Miocene the salinity in this area could not have been as low as it was in the Pliocene and the ancestral hakes could have migrated to the South Atlantic along the coast of Brazil. If true, migration pathways of hake would be different from those proposed by Inada.

Both the works of Inada (1981) and Kabata and Ho (1981) indicated that European hake *M. merluccius* occur in the region of the North Atlantic inhabited by the original stock (Fig. 1). However, the phylogenetic hypothesis (Fig. 3) implies that European hake is the most derived species among the eastern Atlantic hakes, and, consequently, could not be the one occupying the original habitat (Hennig 1966, Wiley 1981).

Before discussing further the biogeography of hake inferred from the phylogenetic hypothesis given in Figure 7, some points about the nature of the movement and range expansion of hake need to be explained.

Hakes of the genus *Merluccius* are coastal inhabitants occurring in the waters above the continental shelf and slope. Most species exhibit a seasonal onshore-offshore bathymetric migration correlated with water temperature. Adults and juveniles move inshore during the spring. When winter cooling occurs on the shelf, they migrate to warmer waters on the continental edge and slope (Grinols and Tillman 1970). Additionally, the silver hake and Pacific hake apparently undertake a latitudinal migration (Bailey et al. 1982, Leim and Scott 1966, Nelson 1969). During the fall they move southward and then return to more northerly waters during the late spring. Clearly, paleotemperature changes in the ocean could be one of the factors in altering the limits of the distribution of hake in the past: they expanded onto the continental shelf or slope of lower latitudes when there was a cooling trend, and retreated to the waters of higher latitudes when the cooling trend subsided.

The copepod parasite *Neobrachiella insidiosa lageniformes* has been recorded from widely separated species of hake, e.g., the silver hake off the coast of Florida and the New Zealand hake in the western South Pacific (Kabata and Ho 1981). Since this parasite is found mostly on the adult hake, rarely on juveniles and never on the larvae, the dispersal of this parasite from North America to New Zealand via the South American coast must have been effected by the adults. Besides, this parasite belongs to the family Lernaeopodidae which is noted for a brief stage of free-living during development. It is logical to assume that adult hakes, not larvae, are responsible for extending their range.

The offshore hake *M. albidus*, primarily an inhabitant off the U.S. east coast and in the Gulf of Mexico and Caribbean (Inada 1981), does not share its clade with any extant hake (Fig. 7). The distributional ranges of its ancestor must have waxed and waned like other ancestral hakes with the changes of ocean temperature and sea level. However, it is very likely that this stock of hake stayed mostly in the Gulf of Mexico and

Caribbean for most of the time since its evolution in the Eocene.

Geologic events that cause fragmentation of the contiguous, ancestral distribution are considered the major means of distributional pattern formation (Nelson and Platnick 1981). Although not all vicariant events are identifiable at present, those known geologic events that could have produced the present pattern of hake distribution are explored below.

Range expansion and vicariance of species B

The closeness between fossil members of the genera *Palaeogadus* and *Merluccius* has led Fedotov and Bannikov (1988) to speculate that hake originated from a species related to *Palaeogadus intergerinus* in the Middle Miocene. However, since fossil records indicate the minimum age, the discovery of fossil *Merluccius inferus* from the Tethys area of the Soviet Union in the Middle Oligocene deposit may not necessarily signify that *Merluccius* originated in the Middle Oligocene. The genus could have made its appearance much earlier. It is unclear when the hakes living on the western North Atlantic seaboard (off North America) diverged into two stocks, but species B must have expanded its range southward and moved into the continental shelves of low latitudes in the late Eocene (about 40 million years ago [MA]), an age characterized by a major decrease in annual temperature (Frakes 1979, Wolfe and Poore 1982). According to Savin et al. (1975), equatorial temperatures may have been as low as 20°C throughout the Oligocene (35–25 MA); consequently, species B most likely migrated into Brazilian waters during this long cooling period.

In his discussions on Caribbean biogeography, Rosen (1975, 1978, 1985) concluded that there was an isthmian land bridge between North and South America in the late Cretaceous or early Cenozoic. A similar intercontinental link was also suggested by Savage (1966, 1982), Axelrod (1975), and White (1986) in their biogeographic studies on the herpetofauna, plants, and silverside fishes, respectively. Alternatively, recent geologic reports suggested that this isthmian link was most developed sometime in the Eocene (Coney 1982, Pindell and Dewey 1982). In that case during their southward range expansion, hakes of the species B would have been prevented from entering the Pacific.

The area cladogram (Fig. 7) obtained from the adopted phylogenetic hypothesis (Fig. 3) indicates that species D had expanded across the Atlantic Ocean to become the common ancestor of hakes in the eastern Atlantic. The occurrence of such range expansion would invoke a geologic event with a shallow-water (<200 m) connection between South America and Africa, because, from the parasitological point of view, it is the demersal adult hakes (and not the planktonic larvae) that are responsible for this range expansion. Since the fossil hake *Merluccius inferus* is known from the middle Oligocene deposit in Europe (Svetovidov 1940), this eastward crossing of the Atlantic must have occurred in the early Tertiary. However, no such extension of continental shelf in the Tertiary has been proposed by geologists, except Vail et al. (1977) who recognized five major lowstands in the Tertiary (Mid-Paleocene, Early-Mid Eocene, middle Late Oligocene, Late Miocene, and Late Pliocene-Early Pleistocene). According to them, during these lowstands the sea level fell below the edge of the continental shelf in most regions; thus, the eastward expansion of species D across the Atlantic Ocean in the low latitudes was possible. After reaching the eastern Atlantic, it spread north and south along the coast of Africa.

In the Early Miocene between 22 and 20 MA, the prolonged cooling trend initiated in the late Eocene was reversed (Haq 1982). Temperatures in low latitudes rose to modern values and might have exceeded 30°C in some areas. This change in global climate, even if it did not affect the adult hakes because of their preference for deep water (Grinols and Tillman 1970), could have effectively prevented hatching of their eggs (normally at 11–14°C) and the normal growth of their epipelagic larvae (found usually at 40–60 m); thus, the hakes were prevented from occupying waters of low latitudes. This unusual warming of the tropical waters can be viewed as a vicariance event that split species D into a northern segment which later developed into another ancestral form (species E, Fig. 7), and a southern segment representing the common ancestor (species F, Fig. 7) of the shallow-water and deep-water cape hake. Species E must have invaded again the waters of low latitudes during another cooling, which started in early Middle Miocene (about 15 MA) when a major enlargement of the East Antarctic ice-sheet developed (Savin 1977, Woodruff et al. 1981). This would account for the presence of Benguelan hake *M. polli*, one of the decendants of species E, in the tropical waters of the eastern Atlantic. However, further divergence of species E is unclear given the present knowledge of geologic history.

The ancestor of New Zealand hake *M. australis* is a sister group of species D. It must have occupied the continental shelf off Argentina when the latter crossed the Atlantic. The extinct hake *Merluccius fimbriatus*, known from the Miocene deposit in Victoria, Australia (Stinton 1958), may be a descendant of this stock since the Drake Passage had remained open since the Oligocene, between 29 and 28 MA (Haq 1984). According to Inada (1981), there are two distinct populations of New Zealand hake: the New Zealand population living in New Zealand waters, and the Patagonian

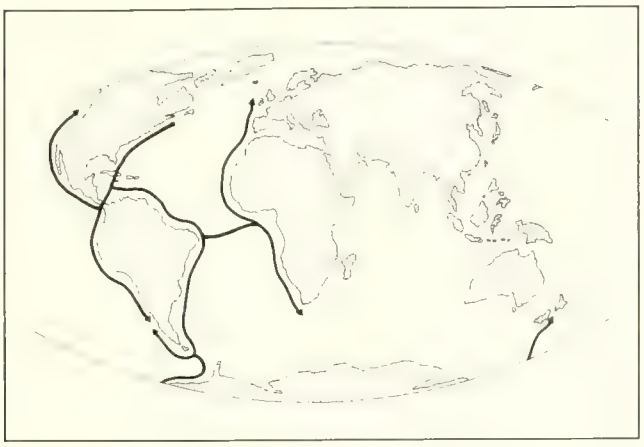

Figure 8
Dispersal routes of hakes inferred from the area summary cladogram in Figure 7.

population living on both sides of the southern part of South America south of 40°S. Interestingly, both populations, in spite of being distantly separated by the Pacific, carry the same species of copepod parasite—*Neobrachiella insidiosa lageniformes*—on their gills (Kabata and Ho 1981), a clear indication that the New Zealand population must have originated from the hakes in South American waters.

Range expansion and vicariance of species C

According to the proposed history of the relative motion of the plates in the Gulf of Mexico/Caribbean region, Pindell and Dewey (1982) concluded that the large-scale eastward migration of the Caribbean plate started in the Oligocene (about 36 MA) and eventually placed the Greater Antilles in their present positions. It is assumed that species C, as in species B, expanded southward prior to the initiation of this Caribbean plate movement. However, being a northern population, it did not reach as far south into the South Atlantic as Species B. Instead, it expanded into the Pacific when the Panamanian seaway was opened in the Oligocene.

As with the hake in the eastern Atlantic, species C was prevented from inhabiting the waters of low latitudes when the climate warmed in the Early Miocene. By this restriction, species C was divided into an Atlantic population, which eventually gave rise to silver hake *M. bilinearis* and a Pacific population (species G, Fig. 7) which became the ancestor of the three eastern Pacific species. The fossil remains of the Pacific hake *M. productus* are common in the Pliocene deposit of California (Fitch 1969, Fitch and Reimer 1967, Zinsmeister 1970), indicating that the divergence of species G into species H and Pacific hake (*M. productus* or its immediate ancestor) took place either in Miocene or Pliocene.

Species H was very likely confined to the North Pacific off the coast of Mexico until the Pliocene when the Panamanian isthmus was reestablished at about 3 MA (Haq 1984). Panamanian hake *M. angustimanus* is found from Baja California to Colombia, but not in the Caribbean; therefore, species H must have moved southward after closing of the Panamanian seaways. The vicariance event responsible for the separation of species H into Panamanian hake and Chilean hake is unclear, but the influence of the Ice Ages during the late Pliocene and Pleistocene may have played a role.

Conclusion

The phylogenetic hypothesis of hake (Fig. 3) presented here is the most parsimonious scheme derived from the cladistic analysis of the osteological data of Inada (1981). It is congruent with the scheme of evolution proposed by Ho (1974) for the hake-specific copepod parasites. This is a testable model; it can be corroborated by including more anatomical data (e.g., musculature), ontogeny, karyology, DNA sequences, and allozymes. Parasitological information from protozoans, helminths, and crustaceans can also provide further corroboration, particularly when hake-specific parasites are found among them.

The vicariance model proposed for the hake biogeography is based on the adopted most-parsimonious tree that shows congruence with the available parasitological information. The inferred pattern of biogeography, particularly the track across the Atlantic in the low latitudes (Fig. 8), is yet to be reported for demersal fishes. However, it should be mentioned that Van der Spoel and Heyman (1983) considered that the planktonic faunas of the Panama Passage and South American inland sea as ancestral to all eastern Atlantic distant neritic taxa, and proposed a similar eastward dispersal.

The ranges of ancestral hake waxed and waned with the fall and rise of paleoceanographic temperatures in the Tertiary, dispersed during the cooling periods and fragmented by the development of warming trends. Development of major lowstands in sea level is also viewed as an effective vicariant event. This model can be tested with additional details of the plate-tectonic models and paleoceanographic-climatic history. Works on other marine life with similar distributions would test the validity of the three inferred general tracks.

Both the phylogenetic hypothesis and biogeographic model differ from current views, but they are viewed as the better explanation of available data. They are presented here as a working model subject to modification as more exact information becomes available.

Acknowledgments

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Appendix 1

Coding of osteological characters for the hake species (Imada 1981).

Character	States of character (code)
Gill raker length	0: short 1: medium (10)(19)(23) 2: long (11)(20)
Size of teeth on jaws	0: small (22) 1: large (4)
Hyomandibular intermuscular process length	0: none 1: short (1)(21) 2: long (5)
Postcleithrum head	0: large (7) 1: medium (2)(14) 2: small (9)(12)(16)
Urohyal	0: thin 1: thick (17)
Cleithrum groove	0: none 1: deep (3)(15) 2: shallow (13)(18)
Infraorbital foramen width	0: wide 1: medium (6) 2: narrow (8)

Appendix 2

Matrix of character states in the twelve extant species of hakes.

Character	Species 1	2	3	4	5	6	7	8	9	10	11	12
Gill raker length	0	1	0	1	2	2	0	2	2	2	0	0
Size of teeth on jaws	1	0	0	1	1	1	0	0	0	0	1	1
Hyomandibular intermuscular process length	2	2	2	1	2	1	1	1	1	1	2	2
Postcleithrum head	0	0	0	0	0	2	2	2	1	1	1	2
Urohyal	0	0	0	0	0	0	0	0	0	0	1	0
Cleithrum groove	1	1	1	1	1	1	1	2	1	2	2	1
Infraorbital foramen width	2	2	2	1	1	0	0	0	0	0	1	1

1 *merluccius*
2 *senegalensis*
3 *polli*
4 *capensis*
5 *paradoxus*
6 *bilinearis*
7 *albidus*
8 *productus*
9 *angustimanus*
10 *gayi*
11 *hubbsi*
12 *australis*

Abstract.—During 1986, the National Marine Fisheries Service began conducting long-term research vessel surveys to determine trends in population size of dolphin stocks taken incidentally by tuna purse seiners in the eastern tropical Pacific. Line transect methodology was used by observers aboard two vessels for 120 days each. We assumed the variability associated with the abundance estimates would be relatively constant during the sampling period and investigated (1) annual changes in population size of the northern offshore spotted stock that could be detected within a 5-year (six survey) sampling period, and (2) the number of years required to detect a 10% annual decline with α and β error levels of 10%. The abundance estimate of the northern offshore spotted dolphin stock using the first year's data was 929,000 animals. After 5 years, a minimum 17.6% annual decline could be detected during which 62% of the stock would decrease. A 10% annual decline can be detected in a minimum of 8 years. Data from subsequent surveys will be investigated that may improve our ability to detect smaller annual declines.

Monitoring Trends in Dolphin Abundance in the Eastern Tropical Pacific Using Research Vessels Over a Long Sampling Period: Analyses of 1986 Data, The First Year

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The National Marine Fisheries Service (NMFS) is responsible for assessing the status of dolphins taken incidentally by tuna purse seiners in the eastern tropical Pacific (ETP) (Richey 1976). The status of spotted dolphins *Stenella attenuata* is of special concern because it is the major species taken by the fishery (Smith 1979). Of the three stocks of spotted dolphins, the northern offshore stock has been fished more frequently than any other stock. The four stocks of spinner dolphins *S. longirostris*, and the four stocks of common dolphin *Delphinus delphis*, are also taken. The four stocks of striped dolphin *S. coeruleoalba* and the Fraser's dolphin *Lagenodelphis hosei* are occasionally caught (Holt and Powers 1982). These five species are herein grouped and termed target species.

NMFS conducted assessments of target populations in 1976 (SWFC 1976) and again in 1979 (Smith 1979) using absolute stock abundance. The validity of the absolute estimates depended on several assumptions (i.e., all schools located directly on the trackline were detected, schools did not respond to the ship before being detected, etc.). Unfortunately, not all of these underlying assumptions were met (Holt and Cologne 1987, Holt 1987). Therefore, in 1984 Congress amended the Marine Mammal Protection Act and mandated that an alternative approach for assessing stocks be used that was less sensitive to biases. By using consecutive population estimates and establishing the first estimate as a base to which all subsequent estimates would be relative, we can detect trends in stock sizes over a long sampling period. These relative estimates can provide an assessment of stock condition if the biases in the abundance estimates are consistent over the sampling period.

In 1986, NMFS initiated a research program to monitor dolphin populations in the ETP which would utilize two research vessels for at least 5 years during which six surveys would be conducted. The research design (Holt et al. 1987) indicated that a 10% annual rate of decrease in northern offshore spotted dolphins could be detected (a total 41% decrease over six surveys). Herein, we present the population estimates for the first year's survey data. We also discuss effects of several factors on these base estimates, and, assuming data for subsequent surveys will have the same level of precision (coefficient of variation levels) as the first year, examine changes in population sizes that can be detected in 5 years or, conversely, the number of years required to detect various levels of change.

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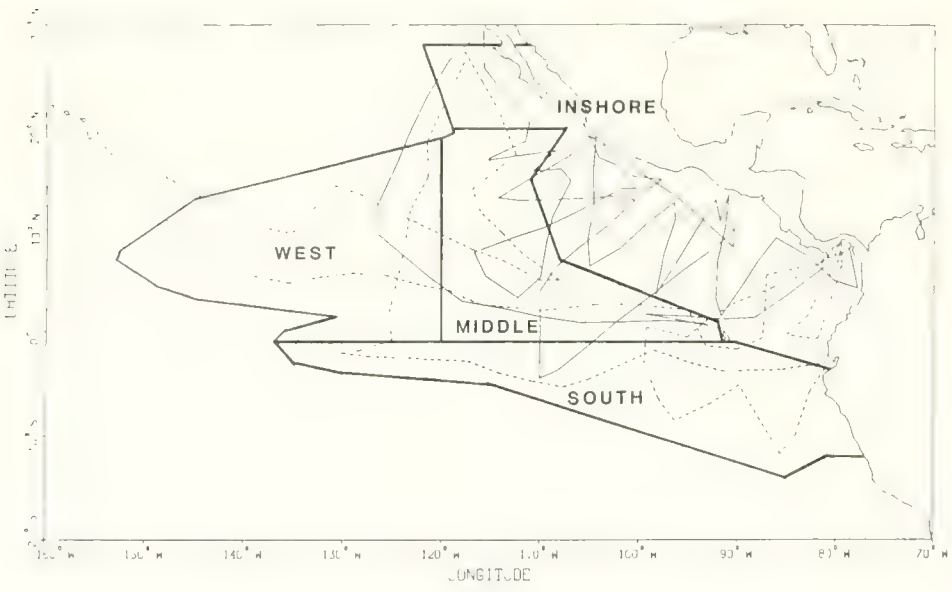

Figure 1
Tracklines traversed by the NOAA RV *David Starr Jordan* (solid) and *McArthur* (dash) during the 1986 dolphin survey, eastern tropical Pacific. Tracklines generated using noontime positions.

Materials and methods

Study area and survey coverage

The study area was described by Au et al. (1979) (Fig. 1). We partitioned the area into four strata: inshore, middle, and west located north of 1°S, and a south stratum. These strata were selected based upon preliminary examinations of historical distributions of dolphin stocks and oceanographic features.

The NOAA research vessels *David Starr Jordan* and *McArthur* traversed predetermined tracklines in the ETP during 29 July–5 December and 6 December, respectively (Fig. 1). Each vessel spent approximately 120 days at sea. Detailed operations, survey procedures and preliminary data summaries for each vessel are presented elsewhere (Holt and Sexton 1987, Holt and Jackson 1987).

On each ship, two observers used 25× binoculars located on each side of the ship to search from directly ahead to abeam of their respective sides of the ship. A third observer served as data recorder and searched directly ahead of the ship when not recording data. Two teams of three observers each alternately occupied the three duty stations. Each team was on duty for 2-hour shifts. During each shift, members spent approximately equal time occupying each duty station. Whenever possible, schools were approached and observers recorded independent "best" estimates of school size. If an observer could not obtain a best estimate, a "minimum" estimate was made. Independent estimates were averaged to obtain mean minimum and best estimates.

Abundance estimation

Estimates of population abundance of the target species (N_{ij}) are computed as (Holt and Powers 1982):

$$N_{ij} = \sum_{k=1}^{4} [D_k S_{tk} P_{tk} P_{ik} A_k / A_{ik}] [A_{ijk} + P'_{ij} A'_{ijk}],$$

where

D_k = estimate of density of all dolphin schools, both identified and unidentified to species, in area k,

S_{tk} = estimate of mean size of target schools in area k,

P_{tk} = estimate of proportion of dolphin schools which are target schools in area k,

P_{ik} = estimate of proportion of individuals of species i in target schools in area k,

P'_{ij} = estimate of proportion of individuals of stock j of species i in target schools in overlap region containing two stocks of species i (overlap region discussed in text),

A_k = total area inhabited by the target species in area k,

A_{ik} = area inhabited by species i in area k,

A_{ijk} = area inhabited by species i, stock j, in area k, and

A'_{ijk} = area inhabited by species i, stock j, in overlap region of area k.

The variance of N_{ij} was calculated using bootstrapped methods. For each stratum, the number of legs (segment of time during which all sighting

conditions were consistent) of searching effort was tabulated, and then effort legs equal to that number were randomly selected with replacement. This effort and the associated sightings were used to calculate school density, school size, species proportions, and finally estimates of N_{ij}. This process was repeated 100 times. The bootstrapped variance of N_{ij} for each stock was calculated using these 100 estimates.

Formulae used to estimate school density are from Burnham et al. (1980), Holt (1985, 1987), and Hayes and Buckland (1983). The Fourier series (Crain et al. 1979) and hazard rate (Hayes and Buckland 1983, Buckland 1985) models both provided adequate fits to the perpendicular (sighting) distance data; however, the hazard rate model was used because, unlike the Fourier series model, it does not require subjective selection of the number of terms in the model and, therefore, could be used in the bootstrapped procedures. Of schools containing both target and non-target species, only the proportion of individuals of the target species was used in the school size estimates. Estimates of the proportion of all dolphin schools that were target schools (P_{tk}) were calculated using formulae from Holt and Powers (1982). Formulae to estimate the proportions (P_{ik}) of the number of individuals for each species of all target individuals are given by Barlow and Holt (1986).

All species of dolphins encountered in the study area were included in the density analyses. Estimates were calculated using only schools containing 15 or more animals. Smaller schools were not used because we believe small schools both on and off the ships' tracklines may be difficult to detect, especially during rough weather and may have been missed at a variable rate depending on prevailing weather conditions (Holt and Powers 1982).

Schools detected at increasing distances from the trackline tend to include disproportionately more large schools because there is a direct correlation between the size of a school and the probability of it being detected (Drummer 1985). This biases school size estimates upward and species proportions toward species which tend to occur in large schools. We attempted to adjust for this bias by weighting school size and species-proportion estimates by the inverse of the logarithm of school size (Holt and Powers 1982). Schools for which there were no "best" estimates of size were not used in the school-size or species-proportions calculations.

Because a 3.7 km (2.0 nm) truncation point provided the best fit of the hazard model to the data, only schools detected within 3.7 km perpendicular distance of the trackline were used to estimate school density. Schools detected greater than 3.7 km have little affect on the density estimates, and the perpendicular distance distributions of schools at greater distances were "spiked". These spikes are a result of the observers' tendency to round-off estimates of radial distances and sighting angles of schools detected at large distances from the vessel in multiples of 0.5 nm or 5°, respectively.

Some stocks of the same species have overlapping ranges (A'_{ijk}). These overlapping stocks include (1) coastal and northern spotted, (2) eastern and whitebelly spinner, and (3) Baja Neritic and northern common dolphins (Perrin et al. 1984). The relative number of dolphins of each overlapping stock (P'_{ij}) was calculated for data pooled over the range and, if applicable, over strata. The relative proportions of coastal and northern spotted, and of eastern and whitebelly spinner stocks, within their respective areas of overlap, were calculated as the average of their relative abundances (percent occurrence). Few data were available to determine relative proportions of the overlapping Baja Neritic and northern common dolphins. Therefore, population estimates for Baja Neritic were combined with northern common dolphins.

The area inhabited by each target species (A_{ik}) and each stock (A_{ijk}) used to calculate the population abundance estimates were those defined by Au et al. (1979) and Perrin et al. (1984). The size of each stratum (A_k) and the size of the area occupied by each stock in each stratum were calculated by counting the number of 1° quadrilateral squares in the stratum at each degree of latitude; partial squares were approximated. Next, the number of 1° squares was multiplied by the area in a 1° square for that latitude as described by Holt and Powers (1982).

Detecting trends in abundance

The variability associated with the population abundance estimates of northern offshore spotted dolphins during this first survey was examined to determine changes which may be detected from subsequent surveys using methods presented by Holt et al. (1987) and Gerrodette (1987). For Type I (α) and Type II (β) error levels of 0.10, we computed the number of years required to detect a minimum annual decrease of 0.10 and the minimum annual decrease in northern offshore spotted dolphins which could be detected at the end of the planned 5-year (6-survey) period. In addition, we calculated the total population decrease that would occur over the 5-year period given that annual level of decrease.

Results

During the entire survey, observers aboard both vessels searched 30,339 km and detected 1150 marine mammal schools. Dolphins were present in 749 of these

Table 1

Summary of 1986 dolphin survey in eastern tropical Pacific. Data were truncated at 3.7 km perpendicular distance. Schools with less than 15 animals were omitted from analyses. School sizes and species proportions weighted by inverse of logarithm of school size. Effort collected during sea states 0–5 were included in analyses. Data summed for both vessels. Total estimates calculated using effort summed over all four strata.

	Inshore	Middle	West	South	Total
Survey area (1000 km^2)	5,693	3,798	5,298	4,359	19,148
Percent of total survey area	30	20	28	22	100
Trackline searched (km)	11,889	7,846	3,877	4,056	27,669
Percent of searching effort	43	28	14	15	100
Dolphin schools					
Density (D_k) (schools 1000 km^{-2})	3.62	2.56	1.89	2.32	2.89
Number detected	165	77	28	36	306
Mean [illegible] (S_k)	89.41	83.97	104.55	179.04	99.13
Number target schools[2]	126	71	25	27	249
Pr[illegible] (P_k)	0.790	0.906	0.897	0.744	0.825
Proportion of target animals by species					
Spotted	0.239	0.378	0.347	0.170	0.266
Spinner	0.293	0.242	0.351	0.054	0.235
Common	0.296	0.108	0.008	0.661	0.305
Striped	0.163	0.272	0.126	0.056	0.160
Fraser's	0.009	0.000	0.168	0.059	0.035
Proportion of animals in overlap area					
Coastal spotted					0.395
Offshore spotted					0.605
Eastern spinner					0.703
Whitebelly spinner					0.297
Number of schools in overlap area					
Spotted					29
Spinner					96

[1]Includes unidentified dolphin schools.
[2]Includes schools identified as target species but for which a best estimate of school size was not made.

schools. While searching in the study area (Fig. 1), observers on both vessels searched 27,669 km and detected 306 dolphin schools containing 15 or more animals located within 3.7 km perpendicular distance of the trackline during Beaufort sea states of 5 and less (Table 1). The amount of effort and schools detected varied among strata; 43% of the total trackline searched and 54% of all dolphin schools detected were in the inshore area.

Abundance estimation

The estimate of $f(0)$ for data in the total area (pooled) was 0.522. Density estimates (D_k) in the four strata, calculated using the pooled $f(0)$, ranged from 1.89 to 3.62 schools/1000 km^2 (Table 1). Estimates of mean school size (S_{tk}) of target species ranged from 83.97 to 179.04 animals (Table 1). The proportion of identified dolphin schools that included target species (P_{tk}) ranged from 0.744 to 0.906 among strata (Table 1).

The proportions of individuals of all target schools that were spotted dolphins (P_{ik}) in the four strata ranged from 0.170 to 0.378 (Table 1). The proportions of the other target species among strata also varied greatly. For example, the proportion of common dolphins ranged from 0.008 to 0.661 (Table 1). Only 29 spotted dolphin schools were detected in the overlap region of the coastal and offshore spotted stocks. The proportion (P'_{ij}) of these that were offshore spotted dolphins was 0.605 (Table 1). Of 96 spinner dolphin schools detected in the area of overlap of eastern and whitebelly spinner stocks, the proportion of these that were eastern spinner dolphin individuals was 0.703.

The areas inhabited by each stock (A_{ijk}) of each target species (A_{ik}) in each stratum (A_k), and the overlapping areas (A'_{ijk}) inhabited by (1) coastal and offshore spotted dolphins and (2) eastern and whitebelly spinner dolphins, are shown in Table 2.

Relatively, common dolphins were the most abundant species (Table 3). The estimate of 929,000 northern offshore spotted dolphins represented 78% of the estimate of all stocks of spotted dolphins. The coefficient of variation (CV) of the abundance of the northern offshore spotted dolphon stock, CV(N_{ij}), was 0.255. The

Table 2

Area inhabited (km^2) by each dolphin species/stock in inshore, middle, west, and south strata, and in total survey area, eastern tropical Pacific.

Dolphin species/stock	Inshore	Middle	West	South	Total area
Spotted					
Coastal, non-overlapping	113,660			8,557	122,217
Northern offshore, non-overlapping	4,073,493	3,788,767	4,016,325		11,878,585
Coastal and northern offshore, overlapping	909,279				909,279
Southern offshore, non-overlapping				3,175,138	3,175,138
Coastal and southern offshore, overlapping				68,455	68,455
Total	5,096,432	3,788,767	4,016,325	3,252,150	16,153,674
Spinner					
Costa Rican	248,366				248,366
Northern whitebelly, non-overlapping			1,806,239		1,806,239
Eastern and northern whitebelly, overlapping	4,762,844	3,401,601	2,889,195		11,053,640
Southern whitebelly, non-overlapping	9,825	346,337	47,898	2,543,829	2,947,889
Eastern and southern whitebelly, overlapping	190,322			751,964	942,286
Total	5,211,357	3,747,938	4,743,332	3,295,793	16,998,420
Common					
Northern tropical	1,477,237	477,581			1,954,818
Western central tropical	17,886	1,273,546	2,207,221		3,498,653
Eastern central tropical	3,502,375	420,581			3,922,956
Southern tropical	829,881	847,176		1,239,588	2,916,645
Total	5,827,379	3,018,884	2,207,221	1,239,588	12,293,072
Striped					
Northern tropical	1,104,177	681,546			1,785,723
Western central tropical			2,870,874		2,870,874
Eastern central tropical	3,549,019	1,066,116			4,615,135
Southern central tropical	510,371	1,658,074	514,537	3,792,278	6,475,260
Total	5,163,567	3,405,736	3,385,411	3,792,278	15,746,992
Fraser's*	5,211,357	3,747,938	4,743,332	3,295,793	16,998,420
All species/stocks	5,848,469	3,797,734	5,298,266	4,203,366	19,147,835

*Used total spinner dolphin area.

Table 3

Estimates of base population sizes ($N_{.j}$) (10^3 animals) by stock for target dolphin species in total survey area, eastern tropical Pacific. Estimates weighted by size of each stratum.

Dolphin species/stock	N	SE(N)	CV($N_{.j}$)	Dolphin species/stock	N	SE(N)	CV($N_{.j}$)
Spotted				Common			
Coastal	36.0	8.6	0.239	Northern tropical	124.9	39.7	0.318
Northern offshore	929.0	236.5	0.255	West central tropical	42.5	22.2	0.522
Southern offshore	218.5	120.3	0.551	East central tropical	277.3	85.6	0.309
Total	1183.5	365.4	0.309	Southern tropical	943.2	388.8	0.412
Spinner				Total	1387.9	536.3	0.386
Costa Rican	20.9	6.1	0.292	Striped			
Eastern	579.6	192.2	0.332	Northern tropical	92.4	20.2	0.219
Northern whitebelly	333.1	127.5	0.383	West central tropical	99.9	40.7	0.407
Southern whitebelly	83.1	32.9	0.396	East central tropical	230.6	48.6	0.211
Total	1016.7	358.7	0.353	Southern tropical	212.3	62.4	0.294
				Total	635.2	171.9	0.271
				Fraser's	247.9	202.5	0.817
				Total	4471.2	1634.8	0.366

abundance estimate for eastern spinner dolphins was 579,600 animals with a CV of 0.332.

Trends in abundance

Assuming the CV(N_{ij}) for subsequent surveys will be constant during the sampling period, and with α and β errors equal to 0.10, a 10% annual decrease in abundance of offshore spotted dolphins can be detected in a minimum of 8 years. After 5 years, and assuming the CV(N_{ij}) of 0.255 will remain constant, a minimum annual decline of 17.6% may be detected during which a 62% decrease of the offshore spotted stock would have occurred.

Discussion

A biased estimate may be acceptable to detect trends in population changes if the bias is constant among annual surveys and if it results in a more precise estimate. For example, the estimate of school density that was calculated by fitting a detection function to data pooled over all strata is biased upwards because searching effort was not allocated to strata uniformly but proportionately to historical estimates of density. The inshore stratum, which historically had the largest density (Holt et al 1987), received a greater proportion of the searching effort (43% of total effort) compared with its relative size (30% of total area). However, the pooled estimate is more precise than the stratified estimate, and the bias should be consistent during subsequent years.

Our estimate of target school size (99.13 animals, Table 1) was half the estimate from aerial data collected in 1979 (199.8 animals per school) (Holt 1985). Although school size may have declined between 1979 and 1986, our estimate is similar to a previous school size estimate that used data collected 1979–83 aboard research vessels (119.9 animals per school) (Holt 1985). In addition, we used only schools detected within 3.7 km perpendicular distance of the trackline, while the previous aerial and ship studies used schools detected within 11.1 km perpendicular distance (approximate distance to horizon from ship). Our estimate using the 11.1 km perpendicular distance was 111.97 animals per school. The previous estimates from airplanes and ships may have been biased upward because large schools are more likely detected at greater distances than are small ones.

The inverse log weighting factor used to adjust biases in the school-size and species proportion estimates caused by detecting disproportionately more large schools may have over- or undercompensated by an unknown degree. Recent work by Drummer (1985) investigating size biases may be utilized during comparisons of this data and subsequent years' data.

Estimates of the relative proportions (P'_{ijk}) of coastal and offshore spotted dolphins and of eastern and whitebelly spinner stocks in their respective areas of overlap were based on data pooled over all strata and included all schools occurring within 11.1 km (6 nm) perpendicular distance from the trackline; however, they were based on small sample sizes (29 spotted and 96 spinner schools). These estimates may change with collection of additional survey data. However, the proportion of eastern spinner dolphins to whitebelly spinner dolphins in their overlap area was 0.703 during 1986 (Table 1) and was 0.714 when all research vessel data collected from 1976–86 were combined (207 schools).

Our population abundance estimates are intended to serve as the baseline estimates for relative comparisons using data collected during subsequent surveys. When our estimates of northern offshore spotted dolphins are compared with previous estimates, ours are much smaller than those made for data collected through 1979 (2,775,000 animals) (Holt and Powers 1982) and for data collected through 1984 (2,533,300 animals) (Holt 1985). Both the latter absolute and our current base estimates may be biased because they share common data collection constraints—failure to detect all trackline schools—which bias the density estimates downward. The older estimates may also contain other biases which result in relatively higher values. For example, those estimates used a combination of data collected aboard airplanes, research vessels and tuna vessels, and survey coverage was pooled over several years, seasons, and areas. However, some variables used to calculate our estimates used small data sets that may have resulted in less precise results.

Because our population estimates are intended to serve as the baseline estimate for relative comparisons using data collected during subsequent surveys, consistent bias during the sampling period will not jeopardize the results. Therefore, several options will be reviewed in analyzing subsequent years' data which may reduce variability associated with the population estimates. Sample sizes to calculate school sizes and species proportions may be increased by utilizing all schools detected at perpendicular distances from the trackline out to the horizon. We will investigate spotted dolphin abundance estimates using only schools of spotted dolphins. A computerized binocular system (Holt and Sexton 1987) may yield more precise estimates of radial distance and sighting angles to dolphin schools, and we have incorporated use of a ship-based helicopter to obtain aerial photographs of dolphin schools to calibrate observer estimates of school size. Hopefully, some or all of these factors may reduce the CV(N_{ij}) levels to around 12%, as anticipated by Holt et al. (1987) in initial survey design.

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Abstract.– Age and growth parameters of the tropical loliginid squid *Sepioteuthis lessoniana* in eastern Australian waters were determined from statolith growth-ring analysis. Juvenile specimens were captured, maintained alive, and their statoliths were chemically marked *in situ* with either tetracycline or calcein. These chemicals produced a fluorescent mark within the statolith microstructure when viewed under UV light. Statoliths were mounted in thermoplastic cement and subsequently ground and polished. This process allowed rings to be visualized without any further preparation. It was thus possible to validate that distinct statolith rings were formed daily and that less-distinct thinner rings were, in fact, subdaily rings.

The results of the age analysis of field-captured individuals revealed that the population of *S. lessoniana* in the study area grows at a very fast rate. Maturity in both sexes was achieved in less than 100 days. All specimens aged were less than 6 months old. The size of large individuals was within the range of *S. lessoniana* captured in other areas, with size ranges being 75–213 mm and 75–184 mm for males and females, respectively.

Growth rates determined for *S. lessoniana* based on statolith ageing are considerably different from previous estimates based on length-frequency data.

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Age and Growth of the Tropical Nearshore Loliginid Squid *Sepioteuthis lessoniana* Determined from Statolith Growth-Ring Analysis

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Estimation of growth rates along with estimates of age-at-maturity and life span are the key elements in understanding the population dynamics of marine organisms. In many instances, such data are difficult to obtain and approximations often have broad confidence intervals. The provision of accurate age estimates is one method by which reliable data on demographic processes can be obtained. For example, research into fish demography has developed rapidly (for relevant reviews see Pannella 1980, Campana and Neilson 1985, Jones 1986) following the discovery and validation of daily microstructure increments within the otolith (Pannella 1971).

Pelagic cephalopods have many fish-like features, yet differ considerably in fundamental ways with respect to metabolism and growth (O'Dor and Webber 1986). Because of their rapid growth and the lack of population statistics in comparison with fish studies, cephalopods are potentially one of the more interesting targets of demographic analysis. Ageing techniques of pelagic cephalopods, employing statolith microstructure analysis, are currently developing along lines similar to those applied to fish biology. Cephalopod statoliths and fish otoliths are physiologically analogous structures (Radtke 1983). Although statolith growth rings were recognized over 20 years ago (Clarke 1966), it has not been until relatively recently that some detailed microstructure analysis has taken place (see Jackson [1989] for relevant literature).

Ongoing research into cephalopod demography is revealing that many species are short-lived and exhibit rapid growth and early maturity (Saville 1987). These features make cephalopods particularly amenable to ageing using daily growth rings. Recent work on growth and ageing on the small tropical sepioid *Idiosepius pygmaeus* has revealed that very small tropical species can have relatively fast growth and maturity rates (Jackson 1989) compared with previous estimates.

The majority of research on squid demography has taken place in temperate waters. Life spans for large temperate squids are generally believed to be annual (Voss 1983, Natsukari et al. 1988, Amaratunga 1987). It was thus of interest to examine age, growth and maturity parameters of a large tropical cephalopod to see if these parameters paralleled similar work on their temperate counterparts.

The tropical loliginid squid *Sepioteuthis lessoniana* was selected for age and growth analysis. This species is one of the larger tropical nearshore squids, reaching lengths of over 30 cm and occurs throughout much of the Indo-Pacific (Roper et al. 1984).

The environmental distribution of *S. lessoniana* in North Queensland waters includes offshore reef environments as well as nearshore/estuarine habitats. Its distribution thus overlaps that of *I. pygmaeus*.

Materials and methods

The two primary components of this study involved (1) the collection of juvenile *Sepioteuthis lessoniana* specimens, which were maintained alive and stained with tetracycline or calcein to determine statolith ring periodicity, and (2) the collection of field specimens, which were fixed shortly after capture and subsequently used for age and gonad analysis. Thus all age estimates were taken from field specimens that were not exposed to artificial maintenance.

Juvenile *S. lessoniana* were often seen along breakwaters in the Townsville region and occasionally in a local estuary. Specimens commonly sheltered under flotsam or floating pieces of ropes, singly or in schools of up to 20. Juveniles were dipnetted and transported back to the lab for subsequent tetracycline staining and maintenance. Collections were made between May 1988 and February 1989.

Larger individuals for ageing were captured using squid jigs at night off the Picnic Bay jetty (lat. 19°11′S, long. 146°50′E) on Magnetic Island (a continental island ~7 km off Townsville) and the Australian Institute of Marine Science jetty south of Townsville (lat. 19°17′S, long. 147°03′E). Night jigging took place between November 1988 and February 1989.

Squids were aged (i.e., statolith rings counted) and examination of reproductive structures was carried out to ascertain the level of maturity. Maturity was determined by the presence of spermatophores in the spermatophore sac in males and the presence of mature oocytes in females.

Maintenance and tetracycline staining

Captured *S. lessoniana* were transported back to the lab and were maintained in 1500-L and 2500-L round tanks located outside so that squids would maintain normal diel periodicity. Specimens were kept alive as long as possible to provide maximum statolith growth before being sacrificed for examination, although in many instances the maintenance was terminated by death of the squid or sometimes by individuals jumping out of the tank. Squids which survived the first few days of captivity were maintained for between 9 and 39 days. Seawater from a closed recirculating system continually flowed through the tanks. Feeding was *ad libitum*. Common food organisms maintained in the tanks were the crustacean *Acetes sibogae australis* and Ambassid, Mugilid, and Clupeid fish species. On several occasions squids were induced to eat previously frozen prawns. Up to seven squids were maintained concurrently in one tank. Their typical behavior was to hover motionless in a school, aligned in the same direction.

The methods for tetracycline staining were the same as used for *Idiosepius pygmaeus* (Jackson 1989). Specimens were normally stained on the day of capture, and if they survived long enough they were exposed to a second staining at least 9 days later, with an interval of 9–20 days between stainings. In one experimental treatment, five squid were initially exposed for 1.5 hours to 100 mg of dissolved calcein per liter of seawater, and then stained a second time 11 days later with tetracycline (250 mg/L, 2 hours). The calcein staining produced a very faint green fluorescence compared with the very strong more yellow-green tetracycline hydrochloride fluorescence. Exposure to calcein at a higher concentration or for a longer time period is likely to produce more prominent fluorescence under UV irradiation.

Preparation and observation of statolith microstructure

Sepioteuthis lessoniana specimens were preserved in 10% borax-buffered seawater formalin to fix tissues and gonads. All length measurements refer to dorsal mantle length (DML). Statoliths were removed the next day within 12 hours to avoid damage from prolonged exposure to formalin. Statoliths were exposed to a 1% bleach solution for several minutes to remove excess tissue, rinsed in distilled water, dehydrated with 100% ethanol and mounted in the thermoplastic cement Crystal Bond. Crystal Bond was found to be an excellent mountant, as it is completely translucent, does not fluoresce under UV irradiation, and statoliths can be easily manipulated or turned-over because it quickly melts at a low temperature and hardens relatively rapidly after removal from heat.

Statoliths were then ground by hand on wet 1200-grade carborundum paper. The scratches from the grinding were removed by polishing the specimens either by hand on wet suede with 0.05 μ alumina powder, or by using a modified gem polishing machine equipped with a microscope slide-holding arm, in which the statolith was lowered onto a 6-inch rotating disc to which was attached a wet Leco Lecloth impregnated with alumina powder.

Statoliths rings were usually best visualized by grinding and polishing the statolith on the anterior (concave) surface only; however, in some statoliths that were particularly opaque or thick, the ring structure was

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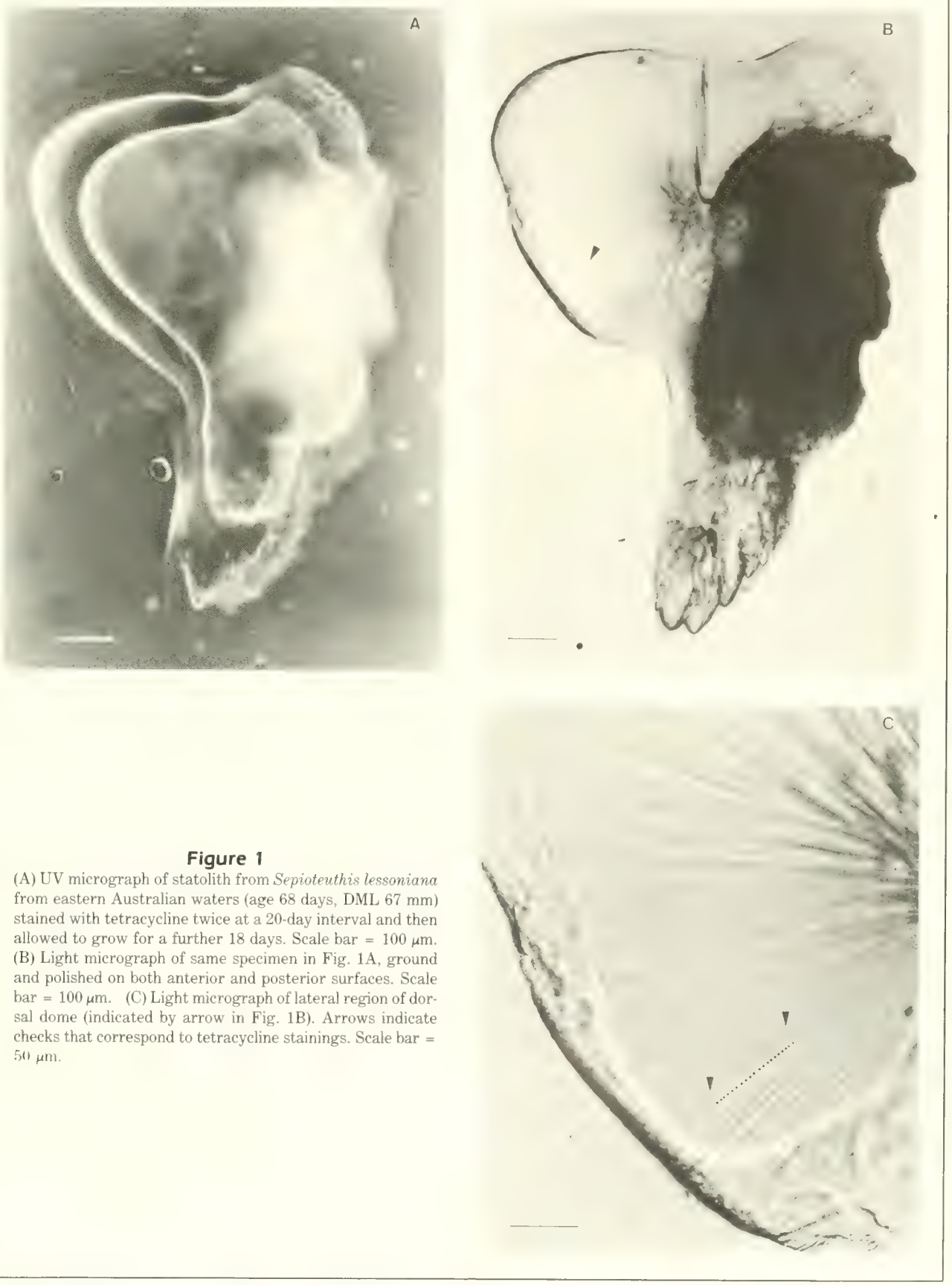

Figure 1

(A) UV micrograph of statolith from *Sepioteuthis lessoniana* from eastern Australian waters (age 68 days, DML 67 mm) stained with tetracycline twice at a 20-day interval and then allowed to grow for a further 18 days. Scale bar = 100 μm. (B) Light micrograph of same specimen in Fig. 1A, ground and polished on both anterior and posterior surfaces. Scale bar = 100 μm. (C) Light micrograph of lateral region of dorsal dome (indicated by arrow in Fig. 1B). Arrows indicate checks that correspond to tetracycline stainings. Scale bar = 50 μm.

Table 1
Statolith ring validation information for *Sepioteuthis lessoniana*.

Mantle length (mm)	Stain 1	Stain 2	Date experiment terminated	Number of days	Number of increments	Comments
53	11 May 88	—	20 May 88	9	9	
50*	18 May 88	—	27 May 88	9	9	
Not taken	14 Oct. 88 (calcein)	25 Oct. 88	8 Nov. 88	11	11	Between stains
52	14 Oct. 88 (calcein)	25 Oc.t 88	9 Nov. 88	11	11	Between stains
73	14 Oct. 88 (calcein)	25 Oct. 99	20 Nov. 88	26	26	From 2nd stain to edge
67	20 Oct. 88	9 Nov. 88	28 Nov. 88	20	20	
50	8 Feb. 89	20 Feb. 89	20 Feb. 89	12	11	Died during 2nd staining

*Development of hectocotylus observed on this specimen.

clarified by grinding and polishing on both surfaces. Growth rings were counted on the polished surface with no further preparation. Rings were accentuated by observing the specimen under polarized light and were enumerated with a hand counter by following the ring sequence with a pencil via a camera lucida. Specimen age in days (i.e., statolith ring number) was established by taking the mean of at least three counts that deviated less than 10%. Specimen age was rounded to the nearest whole number.

The statolith size and shape of a newly hatched *S. lessoniana* were determined from a specimen which was hatched from an egg trawled-up in Cleveland Bay off Townsville. This specimen further provided information on DML at hatching (5.3 mm). Growth rate of aged specimens was thus taken as the increase in mantle length in mm/day minus 5.3 (i.e., DML – 5.3/age).

Results

The notable characteristics of *Sepioteuthis lessoniana* statoliths are a rounded dorsal dome and a relatively long, thin rostrum (Fig. 1B). Unlike the sepioid *Idiosepius pygmaeus* in which rings were most obvious in the lateral region of the statolith (Jackson 1989) or *Loligo* (*Photololigo*) *edulis* (Natsukari et al. 1988) which has a clearly countable ring sequence in the rostrum, *S. lessoniana* statolith rings were most discernable in the dorsal dome. Rings were very difficult to discern in the rostrum.

The ring sequence within the statolith commenced from a prominent check, although some faint ring structure was visible inside this check. This check ring corresponded closely in size to the outer margin of the statolith of the newly hatched *S. lessoniana* (which also had some ring structure at hatching), indicating that this ring represents a hatching check. This feature has also been documented in the loliginid squids *Alloteuthis subulata* (Lipinski 1986) and *Loligo* (*Photololigo*) *edulis* (Natsukari et al. 1988).

Tetracycline staining

The growth ring sequence could be clearly visualized and counted in the vicinity of the tetracycline or calcein marks in seven specimens maintained in captivity. The counts of these specimens corresponded to a daily periodicity in ring formation (Table 1). Rings were generally more easily counted between two stain marks (Fig. 1C) than from the stain mark to the edge, as the edge rings are the most difficult to discern. A statolith check was often induced within the statolith, which corresponded to the date of capture and staining (Figs 1A, C).

When using high magnification or very sharp focus, numerous subdaily rings could be discerned which often made counting of daily rings difficult. This was especially true in areas of the statolith where rings were quite thick (wide). Using a lower magnification or changing the plane of focus helped to delineate the true daily rings that were superimposed over the numerous subdaily rings. A similar phenomena has been shown to exist in the otoliths of the freshwater fish *Coregonus* spp. (Eckmann and Rey 1987).

Age and growth

A total of 23 individual squids were aged (Table 2) to produce a growth curve (Fig. 2) and to ascertain maturity. Growth in *S. lessoniana* is rapid, with a large size reached in less than 6 months. Growth rates determined for larger specimens were considerably greater

Table 2

Variability in replicate statolith ring counts for field-captured *Sepioteuthis lessoniana* specimens. SD = standard deviation.

Specimen no.	Sex	Replicate	Mean	SD
1	J	37, 36, 35	36.0	1.00
2	J	10, 10, 10	10.0	0
3	J	34, 37, 37	36.0	1.73
4	J	37, 37, 39	37.7	1.15
5	J	34, 34, 35	34.3	0.58
6	J	38, 40, 41	39.7	1.53
7	F	191, 190, 182	187.7	4.93
8	M	89, 85, 85	86.3	2.31
9	F	66, 65, 75	68.7	5.51
10	M	67, 67, 67	67.0	0
11	M	62, 55, 62	59.7	4.04
12	M	98, 95, 101	98.0	3.00
13	M	85, 96, 89	90.0	5.57
14	M	85, 77, 81	81.0	4.00
15	M	87, 89, 90	88.7	1.53
16	M	117, 119, 119	117.7	1.15
17	F	53, 57, 54	54.7	2.08
18	F	68, 64, 68	66.7	2.31
19	F	90, 90, 87	89.0	1.73
20	F	121, 122, 119	120.6	1.53
21	M	151, 159, 150	153.3	4.93
22	M	132, 142, 132	135.3	5.78
23	M	55, 57, 41	57.7	3.05

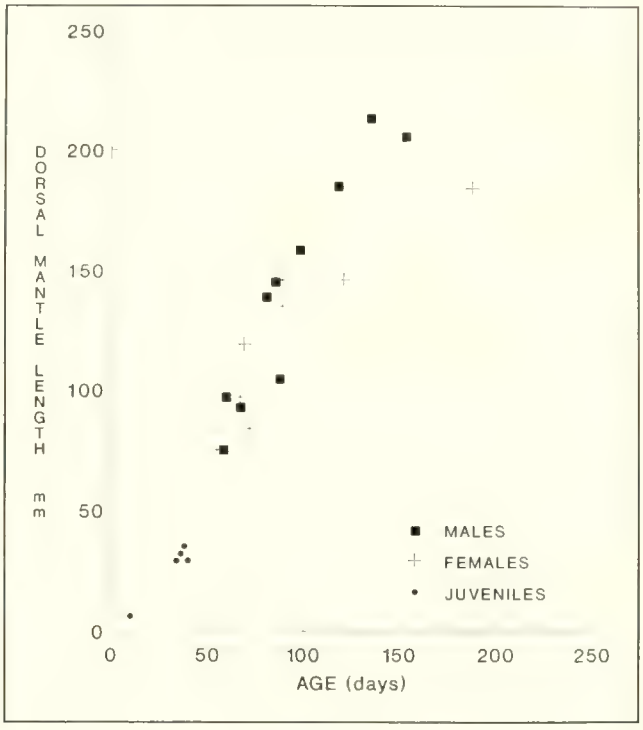

Figure 2

Age-length relationship for field-captured male, female, and juvenile *Sepioteuthis lessoniana*.

Table 3

Age, length, and growth-rate parameters for field-captured *Sepioteuthis lessoniana*. DML = dorsal mantle length; SD = standard deviation.

	N	Age range (days)	DML range (mm)	Growth rate Range (mm/day)	Mean	SD
Paralarva	1	10	6.1	0.08	—	—
Juveniles	5	34–40	29–35	0.59–0.78	0.71	0.073
Males	9	58–153	75–213	1.11–1.65	1.42	0.197
Females	9	60–188	75–184	0.95–1.65	1.34	0.239

than in the paralarvae or juveniles (Table 3). Maturity was found to take place as young as 67 days and 69 days in males and females, respectively.

Discussion

Ageing research with *Sepioteuthis lessoniana* provides further evidence that statolith growth rings in tropical loliginids are a valuable tool that can be applied to tropical squid demography. Daily statolith ring periodicity has also been demonstrated to occur in *Illex illecebrosus* (Hurley et al. 1985, Dawe et al. 1985), *Alloteuthis subulata* (Lipinski 1986), *Loligo opalescens* (Yang et al. 1986), and *Idiosepius pygmaeus* (Jackson 1989). Furthermore, statolith ring sequences have been observed and counted in other temperate-water squid species (Kristensen 1980, Rosenberg et al. 1981, Natsukari et al. 1988).

The presence of subdaily rings within the statolith microstructure of *S. lessoniana* illustrates the need for validation when attempting to enumerate growth rings. Validation is the only way to conclusively delineate whether less-prominent rings are in fact subdaily rings.

Statolith growth-ring analysis suggests that *S. lessoniana* in Australia has a short life cycle and rapid growth. Estimates of age and growth of this species from size-frequency analysis at other localities suggest a very different pattern of growth. Earlier work on growth analysis in India (Rao 1954, Silas et al. 1982) has estimated that *S. lessoniana* takes up to three years to reach maximum size. This has also been further supported by ELEFAN 1 computer program analysis of Rao's (1954) length-frequency data (Longhurst and Pauly 1987).

Data from these different tropical populations of *S. lessoniana* suggest different patterns in the life cycle and growth of this species. The question is raised as to whether this is a locality difference or a reflection of different methodologies in analysis of growth rate.

This study emphasizes the need to critically compare different methods of estimating growth in tropical squids. It is essential to review size-frequency analysis in the light of statolith age findings at a variety of different geographic localities in the range of a species. Growth comparisons incorporating both size frequency and statolith ageing methods of other tropical Australian squid species are currently being investigated.

Artificial culture conditions provide a third method to estimate squid growth. Based on laboratory culture and field observations, Segawa (1987) has reached conclusions similar to the present study of a short life span and rapid growth for *S. lessoniana* in temperate waters around Japan. Segawa further provides growth data from a captive female *S. lessoniana* spawning at 113 days and 143 mm in tropical waters in the Philippines. This value fits well in the size-age correlation for female squid in tropical Australia.

Forsythe and Van Heukelem (1987) have suggested that development and refinement of ageing techniques are the most important tool needed in the study of cephalopod growth in natural populations. While statolith rings are a valuable tool, it is important to use a variety of methods to assess growth on the same population to distinguish between locality and method-specific differences.

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Abstract.– Examination of 95 Dall's porpoise specimens incidentally caught in gill nets, and 4 collected as beach strandings, indicate significant sexual dimorphism and developmental variation in several aspects of external morphology and coloration. The dorsal fins of males become extremely canted in adulthood, and mature males can be distinguished by this feature alone. Size of the postanal hump of connective tissue and caudal peduncle depth also become exaggerated in adult males. The urogenital color pattern is highly variable, and frosting variations on the dorsal fin and flukes can be used to discern the general age of the individual. The strong sexual dimorphism and small testes of Dall's porpoise indicate a polygynous mating system. It is suggested that Dall's porpoise secondary sexual characteristics are used in male-male competition or female choice.

Sexual Dimorphism and Development of External Features in Dall's Porpoise *Phocoenoides dalli**

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Behavioral studies of many mammals have been greatly facilitated by the ability of researchers to distinguish different age and sex classes in the field (see Schaller 1963 for mountain gorillas *Gorilla gorilla beringei*; Geist 1968 for mountain sheep *Ovis dalli* and *O. canadensis*; Schaller 1972 for lions *Panthera leo*; Smith 1988 for mountain goats *Oreamnos americanus*). Knowledge of the behavior and social systems of cetaceans is not as advanced as that of terrestrial mammals, largely due to difficulties in studying these animals at sea and in identifying individuals and age/sex classes (but see Bigg 1982, Bigg et al. 1987 for killer whales *Orcinus orca*).

Dall's porpoise *Phocoenoides dalli* (True, 1885) presents particular problems for behavioral ecologists. It is generally an open-ocean species, seen most commonly several kilometers from shore; lives in small groups that are relatively hard to detect; and is extremely fast-swimming and unpredictable in its movements, often outswimming or evading research vessels. In addition to these problems, detailed studies of sexual and age-related variation in external morphology of Dall's porpoise have not been conducted, and thus identification of different age/sex classes has been limited.

Although few quantitative studies have been done, comments in the literature and my past observations led me to believe that there may be reliable external indicators of age and sex in this species. In particular, five features seemed promising: (1) dorsal fin shape (pers. observ.), (2) caudal peduncle shape (Mizue and Yoshida 1965, Houck 1976), (3) postanal hump size (Scheffer 1949), (4) size of the thoracic epaxial muscle mass (Newby 1982), and (5) coloration patterns, especially the frosting variations of the dorsal fin and flukes (Mizue and Yoshida 1965, Morejohn et al. 1973, Morejohn 1979, Kasuya 1982).

These characteristics were chosen specifically for their potential use in identifying age/sex classes in the field. Another objective of this study was to quantify sexual, developmental, and individual variation in external morphology for use in population studies. Finally, it was hoped that this information, if combined with data on testis weight, would shed light on the type of social system possessed by Dall's porpoise.

Materials and methods

While working as a scientific observer in the U.S.-Japan Cooperative Research Program on Dall's Porpoise, between 12 June and 14 July 1986, I examined 95 Dall's porpoises aboard the mothership *Nojima Maru* of the Japanese high seas salmon driftnet fishery (see description of this fishery in Jones 1984). All of the animals died after becoming inciden-

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Fishery Bulletin, U.S. 88:119–132.

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tally entangled in gill nets set for salmon south of the Near Island group at the western end of the Aleutian Islands, Alaska. The capture locations of these specimens are plotted by 1-degree block in Figure 1. All specimens were of the *dalli*-type color morph (see Houck 1976) and were presumably from the northwestern North Pacific population that calves south of the western Aleutians (Kasuya and Ogi 1987). In addition to these specimens, four calves collected as beach strandings along the California coast in 1987 and 1988 were used in the analyses. Although these four specimens were from a separate population (Kasuya 1982, Kasuya and Ogi 1987), they were included because the sample size of calves was small, and geographic variation at the calf stage was assumed to be insignificant. Little work has been conducted on geographic variation in subadult animals. However, some differences in fin shapes between calves of different stocks of spinner dolphins *Stenella longirostris* have been identified, although these are minor compared with differences in adults (W.F. Perrin, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, pers. commun., Aug. 1989).

Each porpoise was weighed and sexed, a specimen number was assigned, and black-and-white photographs were taken. A series of seven measurements were obtained to the nearest 0.5 cm (Fig. 2, Table 1), and the animal was dissected. The reproductive status of females was assessed as pregnant, lactating, resting, or immature, based on gross examination. The distribution of total lengths of the specimens is shown in Figure 3.

Each specimen was placed into one of seven age/sex classes (Table 2). Most of the classes were based on the total length of the porpoise, generally following the growth curve presented by Newby (1982). Because there was only one neonate male, and only one feature (Canting Index) was measured on it, it was pooled with the females. The assumption was made that there are no sexual differences at the neonate stage. The cutoff between immature and mature males was based on Jones et al. (1987), who gave 180 cm as the average length at sexual maturity. Attainment of sexual maturity in males is considered to be more strongly correlated with length than with age, and all males in this study over 180 cm had enlarged testes, indicative of maturity (Kasuya and Shiraga 1985). Female sexual maturity is not well correlated with length, so average length at maturity was not used to separate immature and mature females. If a female was pregnant, lactating, or had apparent corpora upon gross examination of the ovaries, it was classified as mature. If it fulfilled none of these criteria, but was ⩾151 cm, it was placed into the immature class. Because over 95% of all mature females in the study area are pregnant or lactating during the fishing season, these are very good indicators of sexual maturity for this population (Jones et al. 1983).

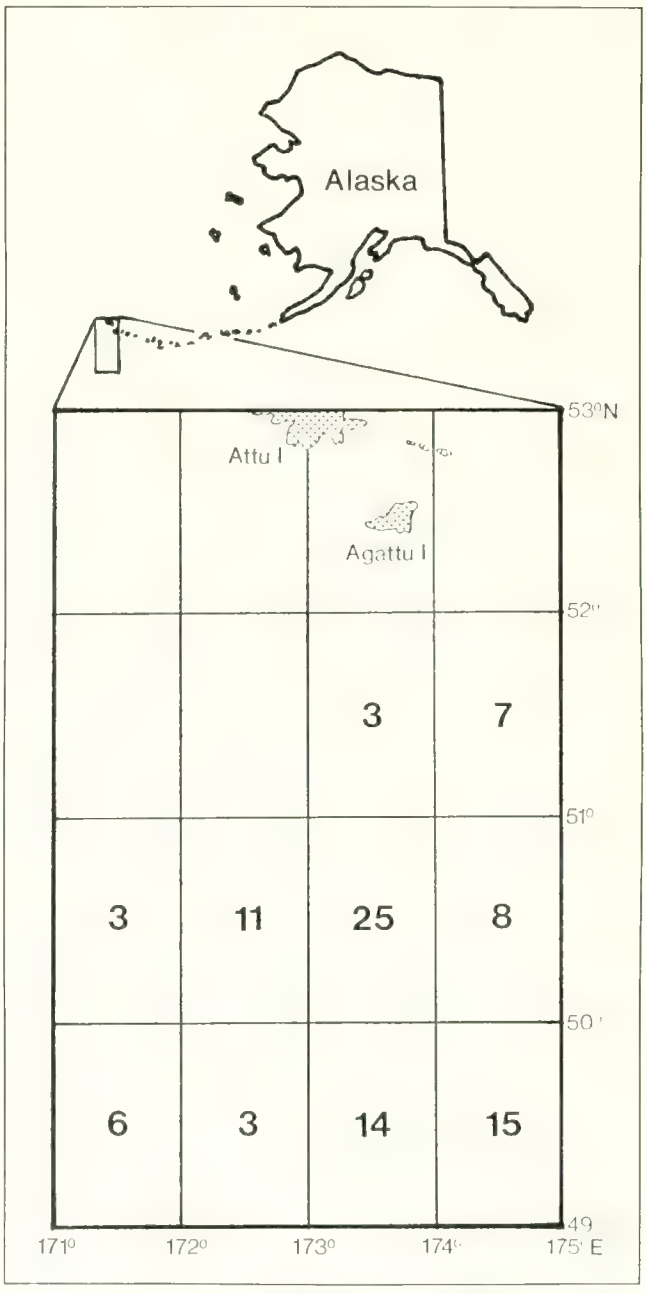

Figure 1
Capture locations of Dall's porpoise specimens from the northwestern North Pacific.

In order to test quantitatively for variation in dorsal fin shape, a value similar to that used by Perrin (1975) for spinner dolphins was computed as the ratio a/b (where a is measurement 7 and b is measurement 6 in Table 1). This quantity is termed the Canting Index, and for Dall's porpoise will generally fall between

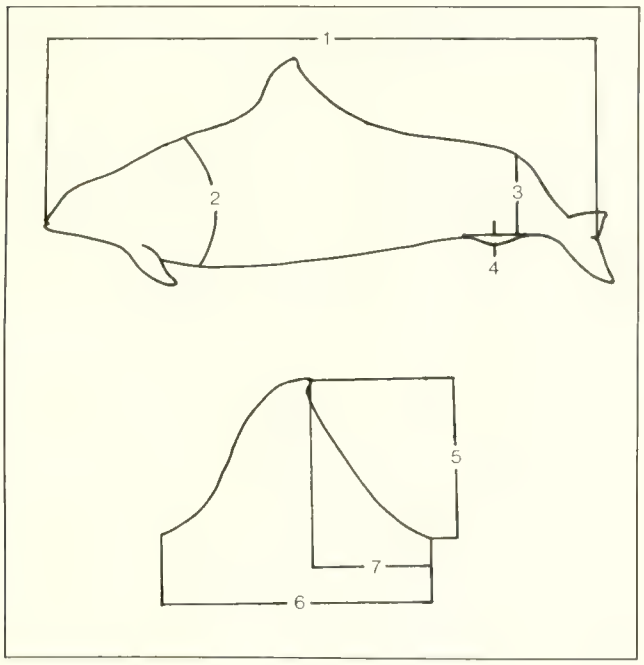

Figure 2
Measurements taken of Dall's porpoise specimens (see also Table 1).

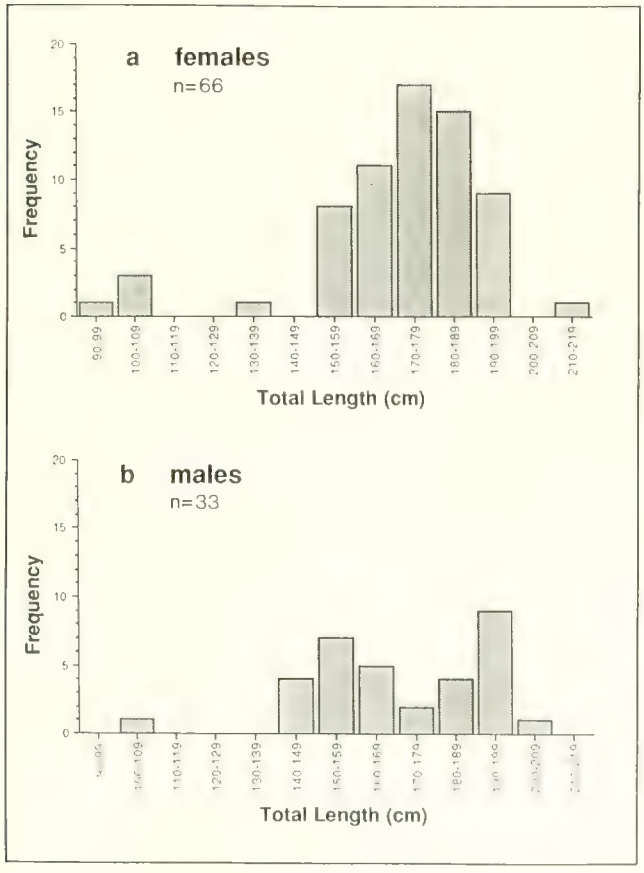

Figure 3
Frequency histograms of total lengths of Dall's porpoise specimens.

Table 1
Measurements of Dall's porpoise specimens taken in this study, illustrated in Figure 2. Numbers in parentheses correspond to numbers of standard measurements in Norris (1961).

No. (Fig. 2)	Measurement
1	Total length (1)
2	Thoractic girth, midway between blowhole and dorsal fin
3	Depth of caudal peduncle, posterior to postanal hump
4	Depth of postanal hump
5	Height of dorsal fin (32)
6	Base of dorsal fin (33)
7	Length from posterior insertion of dorsal fin to a perpendicular from tip

Table 2
Summary of age/sex classes into which Dall's porpoise specimens were separated.

Age/sex class	Symbol	Criteria	*n*
Calf	N	≤130 cm	5
Juvenile female	JF	131–150 cm	2
Juvenile male	JM	131–150 cm	6
Immature female	IF	≥151 cm, not pregnant or lactating, no corpora	16
Immature male	IM	151–180 cm	12
Mature female	MF	≥151 cm, pregnant, lactating, or corpora present	44
Mature male	MM	≥181 cm	14
		Total	99

zero and one. The higher the Canting Index, the larger the degree of foreward canting.

Sexual differences in morphology between immature males and females and between mature males and females were tested with a *t*-test, and age variation was tested separately for males and females with a one-way analysis of variance (ANOVA). Variation in dorsal fin coloration was tested with a chi-square test. Because proportions are known not to be normally distributed, an arc sine transformation was performed on all proportions for statistical analyses (the resulting data approached normality).

Results

External morphology

Dorsal fin shape The dorsal fins of Dall's porpoises cant foreward to varying degrees (Fig. 4). The Canting Index of the dorsal fin shows a tendency to increase

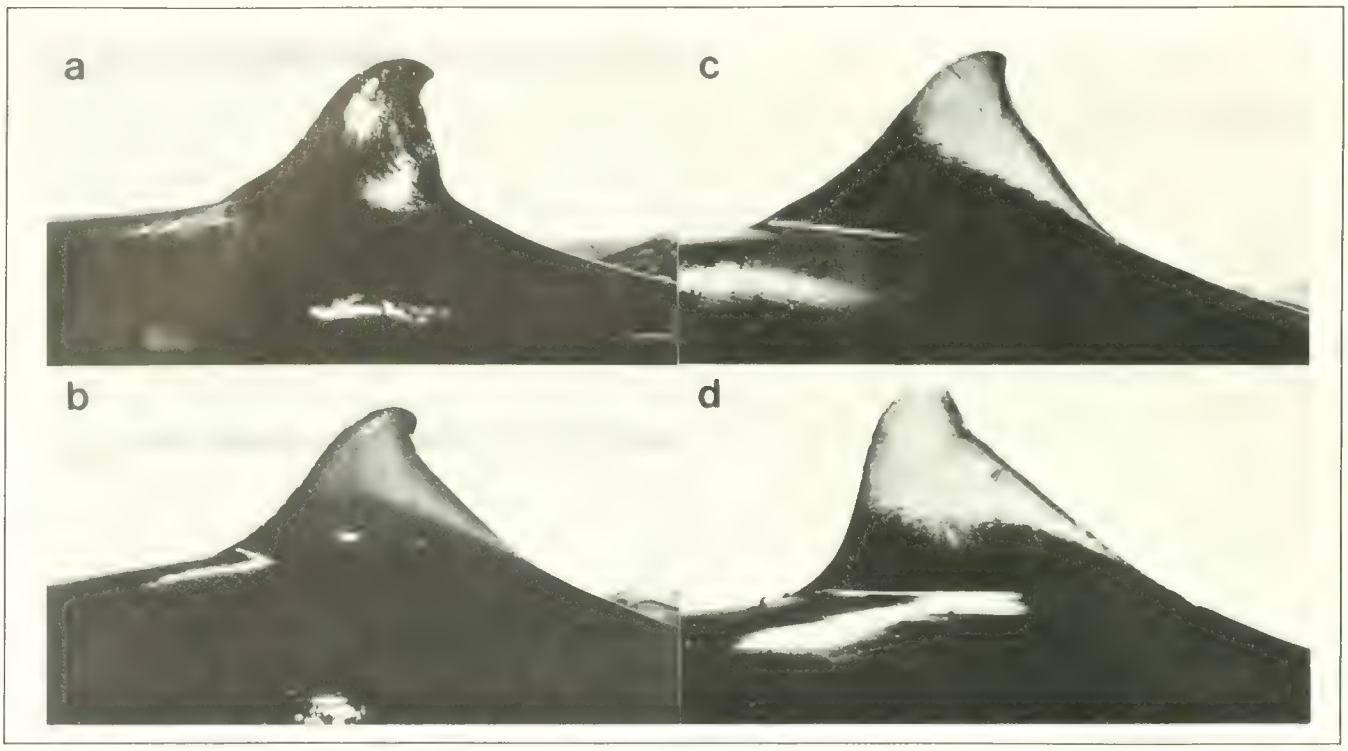

Figure 4
Dorsal fin shapes of Dall's porpoise specimens: (a) calf (TAJ 171), (b) immature male (TAJ 168), (c) mature female (TAJ 156), (d) mature male (TAJ 161).

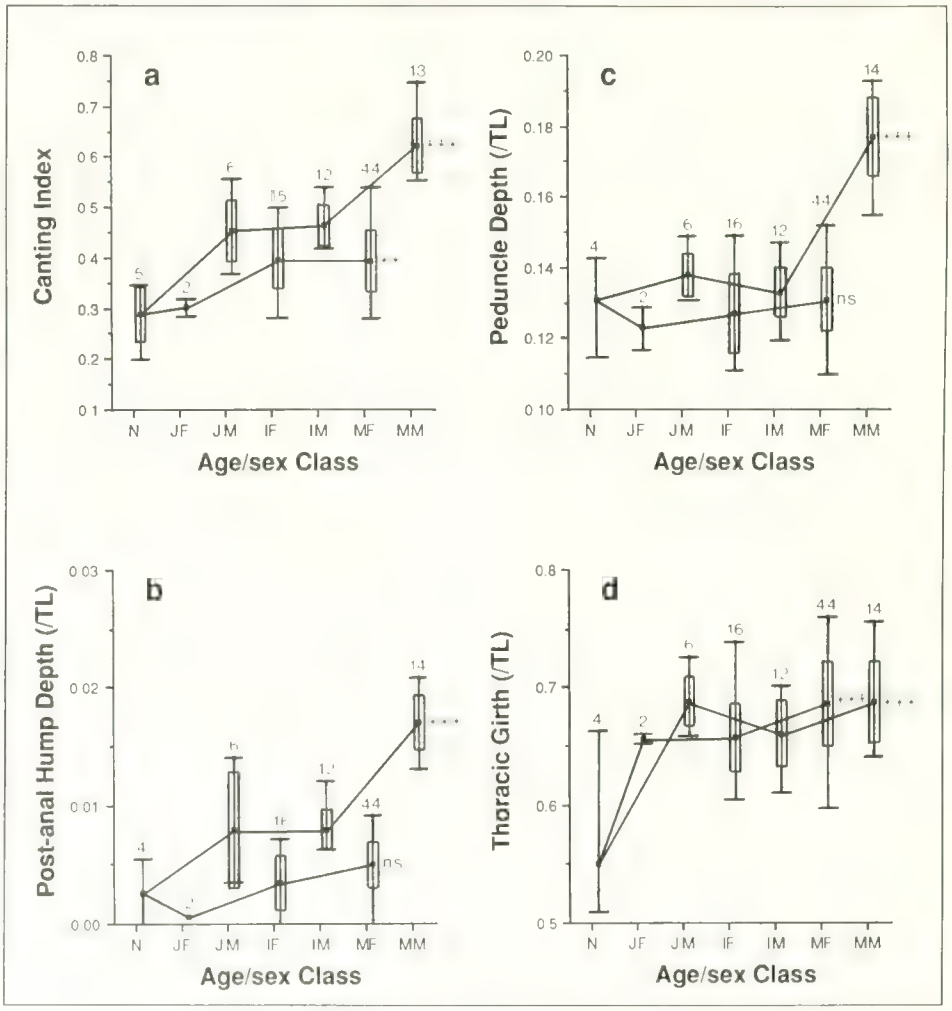

Figure 5
Extern[illegible] features of Dall's porpoise specimens plotted by age/sex class. Points are mean, boxes are ± 1SD, vertical bars are range, and numbers indicate sample size. ANOVAs test for developmental variation separately within each sex: significance *** $p <$ [illegible] significant.

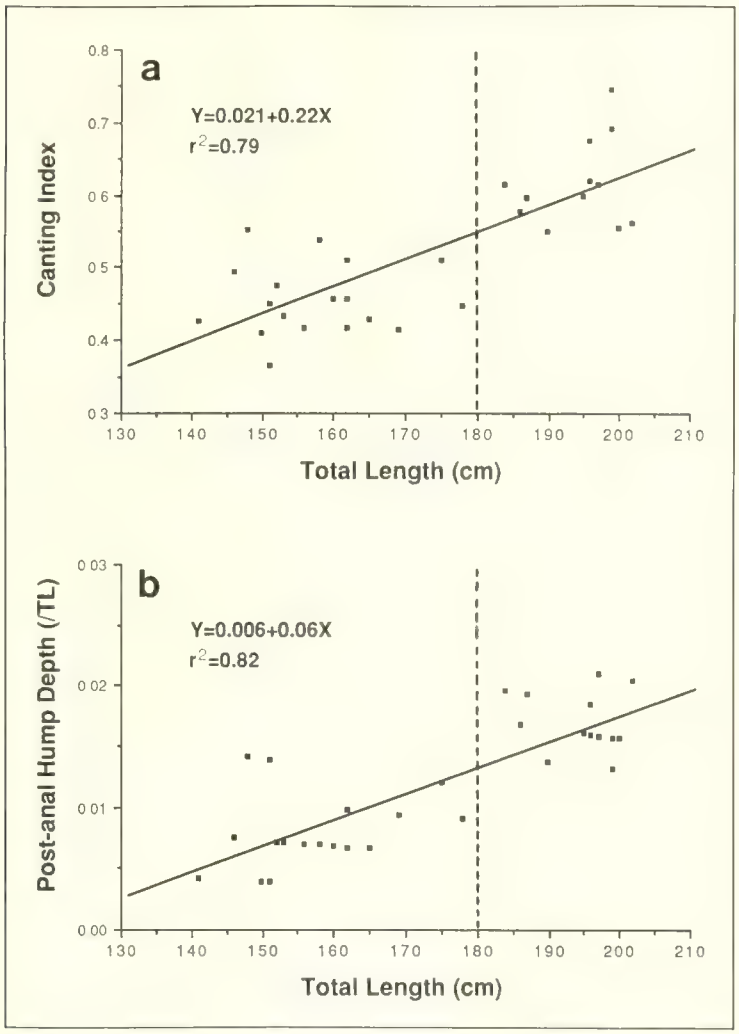

Figure 6
Development of external features in male Dall's porpoise specimens. Broken line represents average length at sexual maturity.

with age of the animal in males (Figs. 5a, 6a). In females, however, the dorsal fin apparently does not change shape once it reaches the immature stage. The difference between the mean Canting Indices for immature males and females was significant ($t = 3.079$, df = 25, $p < 0.01$), and the difference between mature males and females was highly significant ($t = 11.539$, df = 55, $p < 0.001$). In fact, there was little or no overlap between adult males and any other age/sex class, and individuals with a Canting Index of 0.55 or greater can be assumed to be adult males.

At a casual glance, it appears that the dorsal fins of adult males have a wider base than those of females. However, the mean base/height ratio for mature females was 2.15 (SD = 0.18, range = 1.83–2.57, $n = 44$), and for mature males it was 2.16 (SD = 0.15, range = 1.94–2.41, $n = 13$), a non-significant difference ($t = 0.182$, df = 55, $p > 0.05$). The difference in appearance results from the more anterior position of the tip of the fin of adult males, not a wider base.

Postanal hump depth A small to moderate hump composed of connective tissue, just posterior to the anus, could be seen in nearly every Dall's porpoise, including newborn animals. This feature was even evident in most nearterm fetuses.

In some females of all female age classes, the hump was <0.5 cm, and thus not measurable (Fig. 5b). Immature and mature males all had significant postanal humps, but the feature was exaggerated only in adult males, in which it was >1.2% of the total length. Differences between immature males and females ($t = 4.086$, df = 26, $p < 0.001$), and between mature males and females ($t = 8.599$, df = 56, $p < 0.001$) were both highly significant. Postanal hump depth of males increases with increasing length (Fig. 6b), and is correlated with the degree of foreward canting of the dorsal fin (Fig. 7).

Caudal peduncle depth Depth of the caudal peduncle (as a proportion of total length) showed a great deal

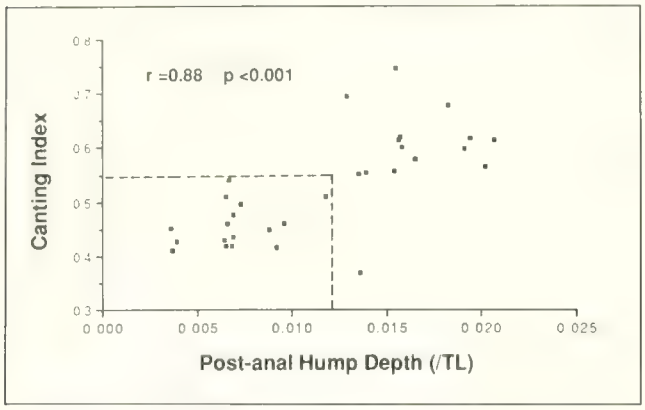

Figure 7
Canting Index vs. postanal hump depth for male Dall's porpoise specimens. Dashed box comprises juvenile and immature males.

of overlap for all age/sex classes, except mature males (Fig. 5c). There was no significant difference in this feature between sexes in immatures ($t = 1.683$, df = 26, $p > 0.05$), but the difference between mature males and females was highly significant ($t = 14.935$, df = 56, $p < 0.001$). The caudal peduncle only becomes greatly deepened in adult males, and again this appears to be an absolute difference. Peduncle depth represents >15% of the total length in mature males, and <15% in all other age/sex classes.

Size of thoracic epaxial muscle mass There was a noticeable "hump" on the back of most adult males examined in this study (Fig. 8f). Dissections of this hump revealed that it resulted from an increase in the size of the thoracic epaxial muscle mass. It did not seem to be asociated with an increase in the thickness of the blubber layer.

Measurement of the thoracic girth in Dall's porpoise was not a good indication of the size of this muscle mass. There was no difference in the size of the thoracic girth (relative to total length) either between immature males and females ($t = 0.245$, df = 26, $p > 0.05$) or between mature males and females ($t = 0.130$, df = 56, $p > 0.05$) (Fig. 5d). After an increase in thoracic girth from the neonate to the juvenile stage, it leveled off in both sexes.

Fluke shape Although no quantitative data were collected on this aspect of Dall's porpoise morphology,

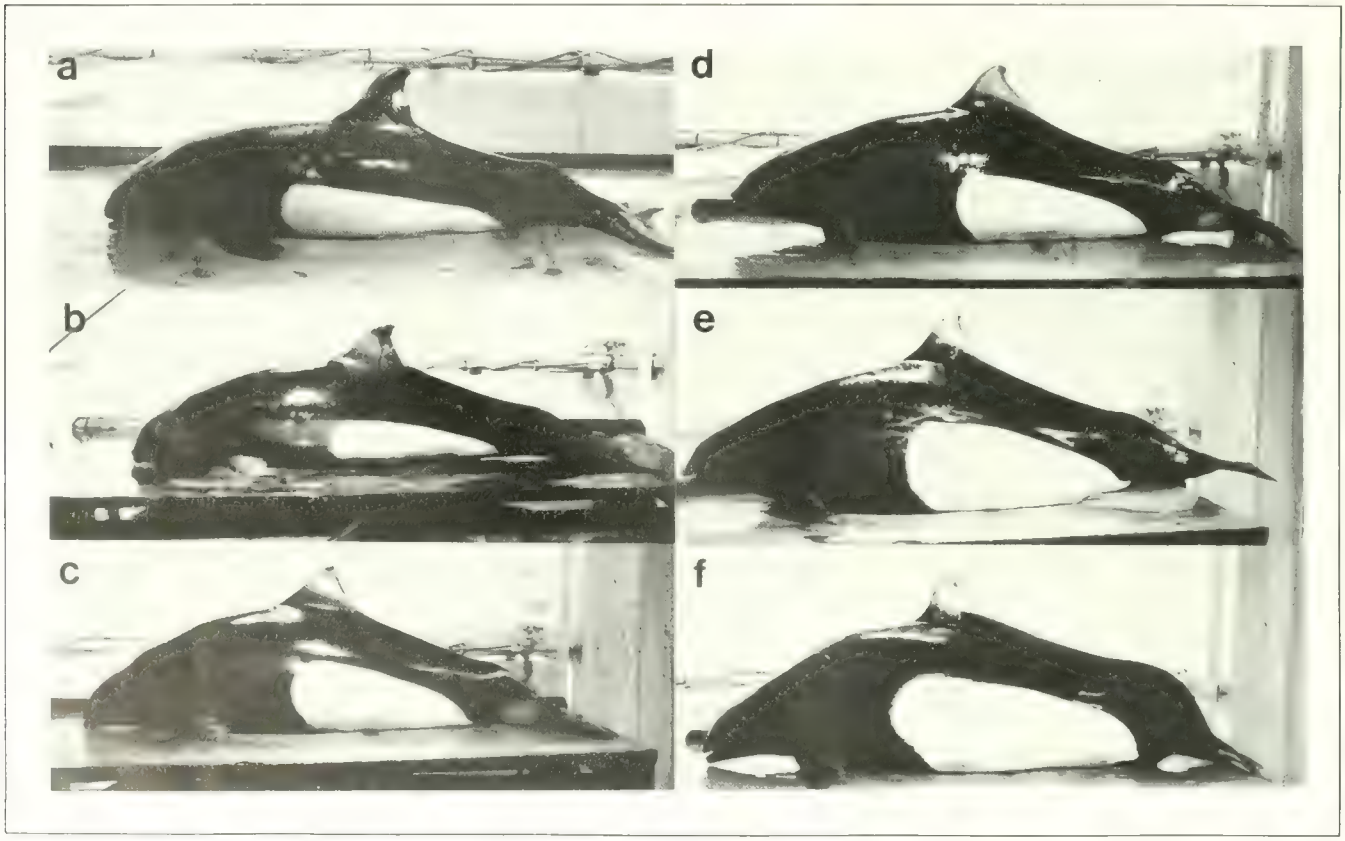

Figure 8
Dall's porpoise age/sex classes: (a) calf (TAJ 171), (b) juvenile female (TAJ 093), (c) immature female (TAJ 162), (d) immature male (TAJ 168), (e) mature female (TAJ 145), (f) mature male (TAJ 150).

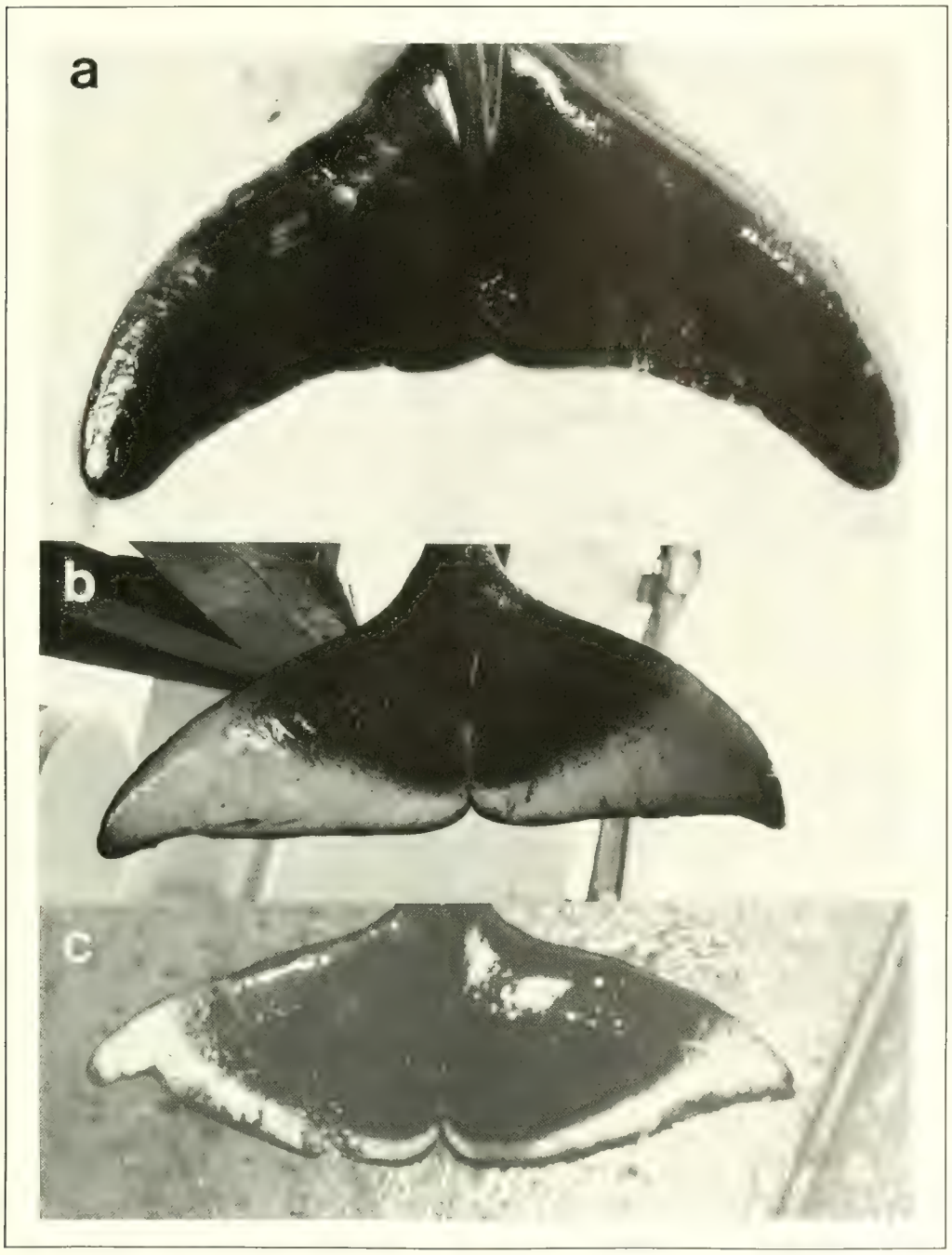

Figure 9
Shape of Dall's porpoise tail flukes: (a) calf (TAJ 171), (b) mature female (TAJ 121), (c) mature male (TAJ 090).

subjective observations suggested that there may be significant sexual dimorphism in the shape of the flukes (Fig. 9).

Newborn porpoises have flukes in which the trailing edge is more or less concave, and the tips are fairly rounded. As age increases, the trailing edge approaches a straight line, and the tips become more pointed and recurved. Some animals have flukes with a convex trailing edge, and these are almost always adult males (animals with extremely convex flukes are always males). There seems to be much individual variability in this feature, however, as some mature males do not have convex flukes. Quantitative data are needed to further explore the relationship between fluke shape and age/sex class.

Coloration

Urogenital color pattern The coloration of the urogenital area of Dall's porpoise has been previously reported to be sexually-dimorphic (Morejohn et al.

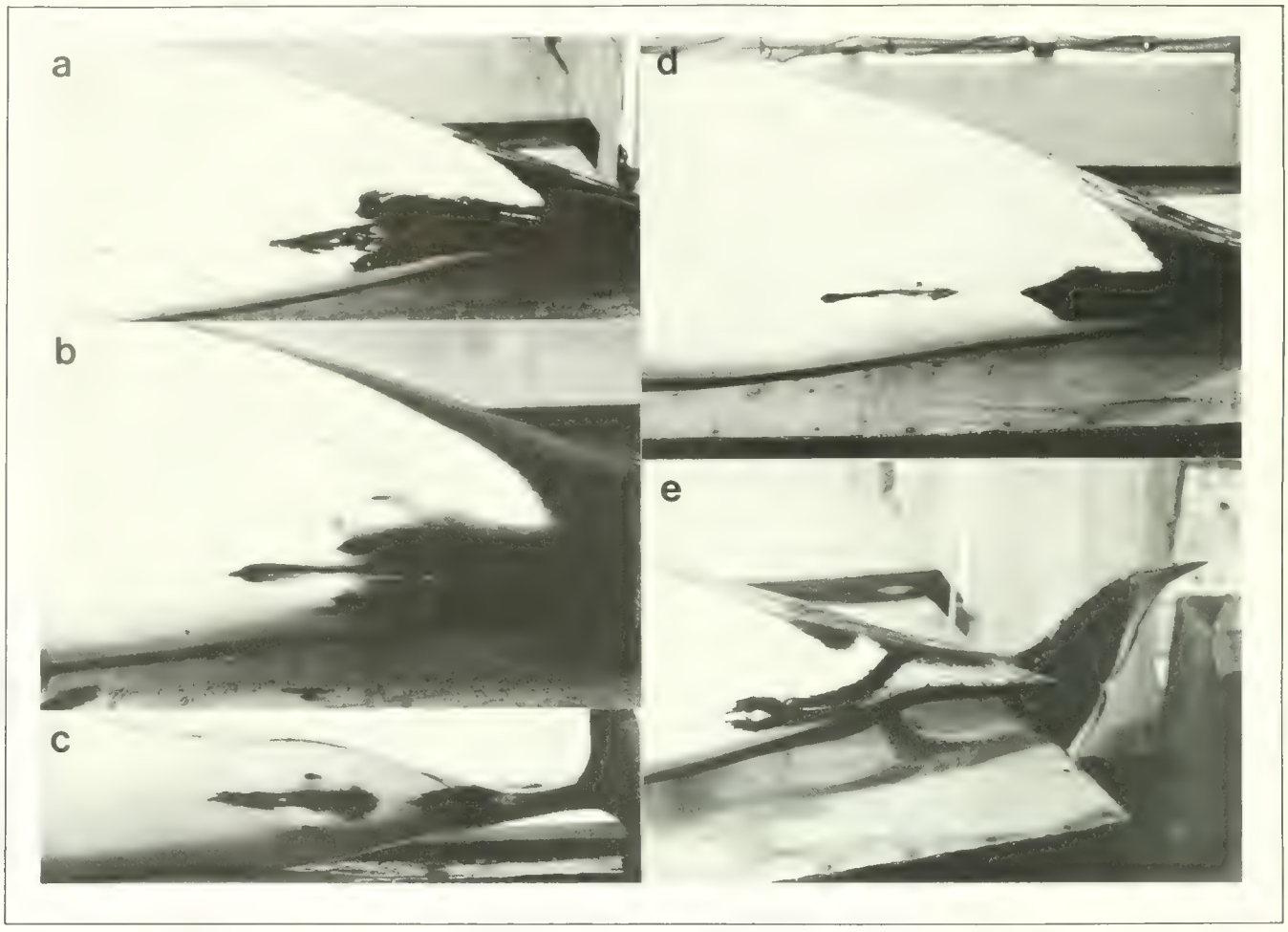

Figure 10
Urogenital color patterns of Dall's porpoise specimens: (a–c) females (TAJ 165, 104; SMB 060), (d–e) males (TAJ 172; WAA 053).

1973). Morejohn and his colleagues illustrated one female and two male patterns, but failed to recognize the large degree of individual variation exhibited by Dall's porpoises in this respect. Figure 10 shows only a few of the many observed patterns. Although most of the patterns can be recognized as more similar to the male or female type, the high degree of variability in this aspect of the color pattern makes sexing individuals by this characteristic alone somewhat risky.

Dorsal fin and fluke frosting A quantitative study of Dall's porpoise coloration may reveal significant sexual differences, but there seem to be no obvious differences between the sexes in any component of the pigmentation pattern, other than urogenital coloration. Analysis of photographs showed that there is, however, a high degree of developmental variation (Table 3). Newborn Dall's porpoises have a muted color pattern of gray tones with no frosting on the flukes or dorsal fin. As the animal ages, the colors apparently inten-

Table 3
Analysis of intensity of dorsal fin frosting coloration in various age/sex classes of Dall's porpoise (H_0: the three categories occur with equal probability). Due to small sample sizes, calves (N), juvenile females (JF), and juvenile males (JM) were not tested.

Age/sex class	Color: No frosting	Color: Gray	Color: White	Statistical test: χ^2	Statistical test: Significance
N	5	0	0		
JF	0	2	0		
JM	0	1	0		
IF	0	9	3	10.500	$p < 0.01$
IM	0	7	1	10.737	$p < 0.01$
MF	0	11	29	29.356	$p < 0.001$
MM	0	3	9	10.500	$p < 0.01$

Figure 11
An example of the type of color pattern of the dorsal fin of Dall's porpoise specimens that can be used to identify individuals. Note the complex pattern of black flecking.

sify and approach the adult black-and-white pattern. Adults of both sexes have white to light-gray frosting on the dorsal fin and both surfaces of the flukes, and many also have light-colored areas on the peduncle, flippers, head, throat, and other areas (see Figs. 4, 8, and 9).

The color pattern of the dorsal fin, in addition to revealing something about the general age of the porpoise, may also be useful in distinguishing individuals. Most adults have an apparently unique pattern of black flecks on the white frosting, which are arranged in what Norris and Prescott (1961) called "flow patterns" (Fig. 11). These flecks tend to be absent or not as well developed in subadults.

Discussion

Identification of age/sex classes at sea

In this section, the results of this study are synthesized with other available information, and a description of how Dall's porpoise age/sex classes can be recognized in the field is given. Age and size ranges of the classes are derived from results of research by the National Marine Mammal Laboratory (Newby 1982; Jones et al. 1983, 1987, 1988). The Canting Index can be measured from a photograph taken perpendicular to the animal slow rolling at sea (Fig. 12).

Sexing Dall's porpoises by genital patch patterns is unreliable. More consistent genital pattern dimorphism apparently exists in killer whales (Bigg et al. 1987), northern right whale dolphins *Lissodelphis borealis* (Leatherwood and Walker 1979), Commerson's dolphins *Cephalorhynchus commersonii* (Robineau 1984, Goodall et al. 1988a), Heaviside's dolphins *C. heavisidii* (Best 1988), Hector's dolphins *C. hectori* (Slooten and Dawson 1988), and possibly Chilean dolphins *C. eutropia* (Goodall et al. 1988b). Despite the claim of Morejohn et al. (1973), using this method for Dall's porpoise would likely result in many incorrect classifications. However, most porpoises fitting the normal male and normal female patterns of Morejohn et al. could be sexed reliably. Those with more variable patterns should be sexed by other means.

Dall's porpoise calves (Fig. 8a) are between 85 and 130 cm in length and less than about 4 months old. Newborns are slate-gray in color, and the flank patch is lighter gray, often with an orangish tinge. Often the flank area just anterior to the flank patch is an intermediate gray. There is generally no frosting on the appendages. Hall (1981) reported that light-gray areas may be seen on the dorsal surface of the head and around the blowhole. The dorsal fin is not canted significantly (Canting Index <0.35). The postanal hump is small to insignificant. The rear border of the flukes tends to be concave, and the head is relatively large compared with the body. Calves are usually in close

Figure 12

An example of how the Canting Index is measured from a photo of a live Dall's porpoise. In this case, the ratio equals 0.67, indicating that this is a sexually mature male.

proximity to an adult, but are rarely seen from boats because cow-calf pairs do not often ride bow waves.

Juveniles (Fig. 8b) are between 130 and 150 cm, and from 4 months to 1 year old. They are significantly lighter in color than adults, and the flank patch is still light-gray. Frosting has begun to develop on the dorsal fin and flukes, but is not extensive and is usually only a bit lighter than the rest of the body at this stage. The Canting Index is between 0.25 and 0.55. A slight to moderate postanal hump may be visible. These animals are most likely weaned, and independent of their mothers.

Immature males and females (Fig. 8c, d) range from about 150 to over 175 cm in females and to about 180 cm in males, but are nearly impossible to distinguish in the field. Females are 1–3 or 4 years old, and males are 1–5. Immatures are very difficult to distinguish from adult females. The color pattern has mostly reached black-and-white, although it may still be somewhat muted. There is usually prominent white to light-gray frosting, and little obvious sexual dimorphism (except that males may have a slighty more canted dorsal fin and a larger postanal hump). The Canting Index is between 0.25 and 0.55. Immatures appear to be the most common bow-riders in many areas.

Mature females (Fig. 8e) are from about 175 cm up to 215 cm long, and more than 3 or 4 years old. The color pattern has reached the adult black-and-white stage, with extensive light frosting on the flukes and dorsal fin; but due to overlap adult females are difficult to distinguish from immatures. The dorsal fin is not strongly canted (Canting Index <0.55). There is usually a small postanal hump. Adult females may be identified if closely accompanied by a small calf. Lactating females and those in late stages of pregnancy often appear to be of extremely large girth.

Adult males (Fig. 8f) are 180 to 225 cm long and greater than 4 years old. The coloration is black-and-white, and extensive white frosting is usually present on the fin and flukes. The dorsal fin is strongly canted (Canting Index >0.55). There is almost always a large postanal hump ($>1.2\%$ of the total length), and the peduncle is deepened ($>15\%$ of the total length). Often, an enlargement of the thoracic epaxial muscle mass is apparent as a hump between the blowhole and the dorsal fin. Many (possibly older) adult males appear to have flukes with a convex rear border, and they are usually very robust (the head may look disproportionately small).

The assumption is made that results from animals of this northwestern North Pacific population are applicable to other Dall's porpoise populations as well. Growth characteristics of reproductively isolated, small cetacean populations are known to sometimes differ

widely (Perrin 1984, Kasuya and Shiraga 1985)l however the same general trends seem to be apparent in photographs of animals from other populations. Only future studies of these features in other *P. dalli* populations will reveal if this assumption is justified.

Sexual dimorphism, testis weight, and mating system

The moderately extreme sexual dimorphism apparent in this species deserves some discussion. Not only are males significantly longer and heavier than females (Kasuya 1978, Morejohn 1979, Newby 1982), but several morphological features are exaggerated in adult males. The mating system of Dall's porpoise is unknown, but sexual dimorphism among mammals, in which the male is larger, is usually related to intrasexual competition for females in a polygynous mating system. In fact, Ralls (1977) determined that extreme sexual dimorphism is a very good predictor of extreme polygyny.

Newby (1982) implied a polygynous system for *P. dalli*, and Landino (1985) suggested a unimale system (either polygyny or monogamy). Landino's prediction is based on the finding that the relative testes weights of various primate species are related to their breeding systems (Short 1979, Harcourt et al. 1981, Harvey and Harcourt 1984). Males with relatively large testes tend to have multimale systems (mostly promiscuity), while those with smaller testes have unimale systems. This is thought to be related to the need to deliver large loads of sperm in promiscuous species, in which the potential for sperm competition exists (see Trivers 1985 for a general description of sperm competition theory). Kenagy and Trombulak (1986) raised the question of whether mating system/testis size predictions apply to cetaceans, but Brownell and Ralls (1986) found sperm-competition theory to be quite useful in explaining mating systems in mysticete cetaceans.

Kenagy and Trombulak (1986) compared relative testis weights for 133 species of mammals, and found the harbor porpoise *Phocoena phocoena*, a closely related species, to have the highest value. This evidence points to extreme multimale (probably promiscuous) breeding for this species, which is consistent with morphological evidence. Harbor porpoises show reverse sexual dimorphism, with females larger than males (Gaskin et al. 1984), and males do not appear to possess any secondary sexual characteristics.

Unfortunately, Kenagy and Trombulak (1986) did not include data on testis weight in Dall's porpoise. In order to compare Dall's porpoise with their information on other species, data on nine adult males presented by Subramanian et al. (1986, 1987) were used in a manner consistent with that of Kenagy and Trombulak. Only sexually mature males taken during the season of male sexual activity were used (August–September; Jones et al. 1988). When plotted on Figure 1 of Kenagy and Trombulak, the Dall's porpoise data point fell close to the regression line for all 133 mammalian species, and well below that of the other five species of small odontocete plotted. The testes of *P. dalli* comprise only about 0.22% of their body weight, as opposed to 4.00% in *P. phocoena*.

Small testes relative to body weight suggests a single-male system with low copulatory frequency (either monogamy or polygyny) for Dall's porpoise. Monogamy is rare in mammals (<3% of all mammal species are monogamous), and it is generally associated with sexual monomorphism (Kleiman 1977). Thus it is unlikely to be the case for *P. dalli*. This leaves polygyny, and this conclusion is further supported by the sexual dimorphism in size (males larger) and the striking secondary sexual characteristics of males in this species. Although some adult males are present, Kasuya and Jones (1984) and Kasuya and Ogi (1987) reported that the majority of mature males are segregated from mating areas during the mating season in the western Pacific. This finding is also more consistent with polygyny than with monogamy.

Several species of odontocete cetaceans show sexual dimorphism in these same charcteristics. For instance, extremely canted dorsal fins are seen in adult male spinner dolphins, especially those of the eastern form of the eastern tropical Pacific (Perrin 1972, 1975). Killer whales and spectacled porpoises *Australophocaena dioptrica* have a significant degree of sexual dimorphism in both size and shape of the dorsal fin (Fraser 1968, Brownell 1975, Heimlich-Boran 1986, Leatherwood et al. 1982). Adult male long-finned pilot whales *Globicephala melas* have more rounded fins, with thicker leading edges than females and young (Sergeant 1962).

Postanal humps appear to be common in many species of odontocetes, although they have been properly described and correlated with age and sex in only a few (published photographs show them in several genera, including *Peponocephala*, *Lagenorhynchus*, and *Lagenodelphis*). Rough-toothed dolphin *Steno bredanensis*, spotted dolphin *Stenella attenuata*, spinner dolphin, and some common dolphin *Delphinus delphis* adult males exhibit prominent humps (Norris 1967; Perrin 1972, 1975; Evans 1975; Leatherwood et al. 1982). Again, this feature is most exaggerated in eastern spinners.

Deepened caudal peduncles (not including the postanal hump) are apparent in photographs of adult male spinner dolphins (Perrin 1972), and Norris et al. (1985) were sometimes able to use this feature to distinguish adult male Hawaiian spinners in the field. To my

knowledge, thoracic humps of the extent seen in adult male Dall's porpoises have not been reported in other cetaceans, but they may exist in a more subtle form in some species. Sexual dimorphism in fluke shape similar to that in *P. dalli* has been reported by Nishiwaki et al. (1963) for sperm whales *Physeter macrocephalus*.

Overall, the dimorphism described here for Dall's porpoise most resembles that described for eastern and whitebelly spinner dolphins by Perrin (1972, 1975). Perrin (1972) proposed that the strikingly canted dorsal fins and enlarged postanal humps of adult male eastern Pacific spinners function as species-recognition signals within mixed schools of spinner dolphins and spotted dolphins. Norris et al. (1985) interpreted these secondary sexual characteristics as signals that make adult males easily recognizable, and possibly allow them to mimic gray reef sharks *Carcharhinus amblyrhynchos*. Subgroups of adult male spinners seem to play an ordering role in dolphin schools, and often achieve this by means of overt aggression. Thus their striking appearance would assist in this aggressive role.

Mating appears to be promiscuous in Hawaiian spinner dolphins (Norris et al. 1985), but understanding the functions of sexual dimorphism seems to be complicated by other social pressures than just mating system considerations. Sexual dimorphism may have originally evolved in association with a polygynous mating system. However, if Hawaiian spinners tended more toward promiscuity than other populations, the sexually dimorphic features might become reduced, but could still function in social ordering (as proposed by Norris et al. 1985). Perhaps eastern spinners have remained strongly polygynous and thus dimorphic, and Hawaiian spinners have moved more towards promiscuity, with whitebellys intermediate.

In this scenario, Hawaiian, whitebelly, and eastern spinner stocks would show a grade of increasing degrees of polygyny and sexual dimorphism, and decreasing testis size. In general, spinner dolphins have relatively large testes (Perrin et al. 1977, Perrin and Henderson 1984). However, eastern spinners have smaller testes than whitebelly spinners, and this is consistent with sperm competition predictions. There is little information on Hawaiian spinners (the form with the least pronounced dimorphism), but if this hypothesis is correct, one would expect them to have the least polygynous system and the largest testes of these three *S. longirostris* races.

I propose that despite the similarity in appearance, the sexual dimorphism in Dall's porpoise evolved and is used largely in polygynous mating. Dall's porpoises do not school with other species, and thus have no need for the type of species-recognition signals suggested by Perrin (1972). Also, Dall's live in small groups, and the need for aggressive ordering of schools is probably nonexistent or very weak.

I have suggested above that *P. dalli* is polygynous, and I believe these sexually dimorphic features are mostly related to male-male competition for females in this species. Newby (1982) first suggested this after discovering that adult male Dall's taken closer to the "rutting season" were heavier, and had a larger thoracic girth, than those taken earlier. The relationship between androgen levels, social aggression, and neck girth has been well established in some polygynous mammals (Lincoln 1971, Bouissou 1983). It is easy to imagine how an increase in size of the thoracic musculature could benefit fighting males, but how the other features could relate to this requires some speculation. If canting of the dorsal fin increases its rigidity, this could aid males that use their dorsal fins in aggressive encounters. A large postanal hump may assist somehow in mating with the female. Of course, these features may not be used in fighting at all, but may instead function as visual signals, allowing males to gauge each other or in being attractive to females, and thus operating in terms of female choice.

It is not possible to evaluate the validity of these speculations at present, because almost nothing is known of the social behavior of Dall's porpoise. Long-term detailed observation of wild porpoises, especially including identification of individuals, is needed to understand how these features operate in wild Dall's porpoise groups.

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Abstract.– We determined the patterns of distribution for eggs and larvae of walleye pollock by analyzing 1,929 ichthyoplankton samples collected on 32 cruises in the western Gulf of Alaska between 1972 and 1986. The combined effects of additions of recently spawned eggs, mortality, dispersion, and advection determine the location and concentrations of eggs and larvae. The vast majority of the eggs were found in spring samples, primarily in April. Larvae were found mainly in late April and May. Eggs occurred mostly in a small area near Cape Kekurnoi in Shelikof Strait, and larvae were centered progressively to the southwest of this area as they grew and were moved by advection. By the end of May, they were usually found near the Semidi Islands. However, comparisions of larval distributions in late May showed significant interannual variations in the area of concentration and larval size.

Egg and Larval Distributions of Walleye Pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska

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Walleye pollock *Theragra chalcogramma* is the dominant gadid in the subarctic Pacific Ocean and in the Bering Sea. It is a moderate-sized (to about 70 cm standard length) pelagic or semidemersal fish that frequently occurs in large aggregations. It feeds primarily on copepods and euphausids, although fish, including its own young, enter its diet (see Lynde 1984).

Intensive multinational midwater trawl fisheries are conducted for walleye pollock in the Gulf of Alaska, the Bering Sea, and the northwest Pacific Ocean. In recent years, catches of walleye pollock have been larger by weight than those of any other single species worldwide (Sharp 1987).

Although pollock spawn intermittently year-round, most spawning occurs in spring. Walleye pollock spawn planktonic eggs that require about 2–3 weeks to hatch, depending on temperature. The planktonic larval period lasts several weeks and the transition to the juvenile stage seems to be gradual. Considerable literature is available on the early life history of walleye pollock, most of it concerning the populations in the eastern Bering Sea (Dunn and Matarese 1987).

From 1972 through 1986, the Northwest and Alaska Fisheries Center (NWAFC, recently renamed the Alaska Fisheries Science Center) conducted plankton sampling in the Gulf of Alaska, primarily in the Shelikof Strait. Based on results of the surveys before 1980, Kendall and Dunn (1985) found that walleye pollock eggs, larvae, and spawning adults were in low abundances throughout the continental shelf and upper slope of the Gulf of Alaska. In spring 1980, however, a large spawning concentration was discovered in Shelikof Strait, and subsequent sampling indicated that spawning occurred there in spring every year through 1988. No concentrations of similar magnitude have been found elsewhere in the Gulf of Alaska, although other areas have not been surveyed as intensively (E.P. Nunnallee, Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070, pers. commun., June 1988).

The migration of spawning adults into Shelikof Strait has been monitored in most years since 1980, and has proven to be quite consistent from year to year (Nelson and Nunnallee 1987). Most spawning in the Shelikof Strait occurs in a localized area in April, as demonstrated by the occurrence of eggs in NWAFC plankton samples. The vertical distribution of walleye pollock eggs in Shelikof Strait shows that a complex pattern of interaction between stage of development and local water density determines their depth of occurrence with a substantial portion occurring below 200 m (Kendall and Kim 1989). After hatching, larvae drift in the upper water column to the southwest during a developmental period of 6–8 weeks (Kendall et al. 1987). This

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early-life-history pattern provides an opportunity to study the recruitment mechanisms of this population.

In this paper, we summarize data on the distribution and abundance of the eggs and larvae of walleye pollock in the Gulf of Alaska, primarily in Shelikof Strait, based on NWAFC sampling from 1972 through 1986. We present this information as a backdrop for detailed studies investigating biotic and abiotic factors that influence the annual survival of these eggs and larvae.

Methods and materials

For our studies, we examined the 32 ichthyoplankton cruises that were conducted by the NWAFC between 1972 and 1986 (Tables 1 and 2). Between 1972 and 1979, 12 such surveys were conducted in various portions of the Gulf of Alaska in all months of the year except January, August, and December (Dunn et al. 1984). Most of the 12 surveys concentrated sampling over the continental shelf southeast of Kodiak Island. Occurrences of walleye pollock eggs and larvae in the 696 tows taken on these surveys were used to investigate their relative seasonal distribution. In 1980, however, when the spring spawning of walleye pollock in Shelikof Strait was discovered, all sampling through 1986 was conducted from March through May with special emphasis in the Shelikof Strait region.

Table 1

Ichthyoplankton cruises in the Gulf of Alaska, 1972–79, with numbers of bongo net tows containing walleye pollock eggs and larvae.

Cruise	Start date	End date	No. stations	Percent occurrence: Eggs	Percent occurrence: Larvae
1MF79	2/13	3/11	88	3	0
4DI78	3/28	4/20	80	36	21
2KE72	4/26	5/9	67	43	36
5TK79	5/16	5/24	58	29	28
2MF78	6/19	7/9	88	1	17
1PO79	9/2	10/11	18	0	0
3MF78	9/9	9/21	24	0	0
4MF78	9/26	10/7	66	0	0
5MF78	10/19	11/1	19	5	0
4MF77	10/31	11/14	59	14	7
1WE78	10/25	11/17	86	3	0
6MF78	11/8	11/16	43	0	0
Total no. stations			696	91	76

Table 2

Ichthyoplankton cruises in Shelikof Strait, March–May, and catches of walleye pollock eggs and larvae. See Appendix 1 for calculations of mean and standard error.

Cruise	Start date	End date	No. stations	Eggs: Percent occurrence	Eggs: Mean no. per 10 m²	Eggs: SE	Larvae: Percent occurrence	Larvae: Mean no. per 10 m²	Larvae: SE
1MF81	3/12	3/20	31	81	334	148	0	0.0	0.0
1SH81	3/17	3/30	46	30	205	116	2	0.2	0.2
4CH84	3/29	3/31	39	97	177,000	39,000	8	3.9	2.2
2MF81	3/30	4/8	89	92	61,000	24,900	24	6.2	2.3
1PO85	3/30	4/13	89	86	28,800	9,020	36	141	112
1MF85	4/3	4/11	84	98	46,300	5,720	3	138	55.0
5CH84	4/4	4/8	58	95	117,000	28,100	59	311	90.3
1MF86	4/5	4/12	79	100	25,100	3,170	91	342	94.0
1DA82	4/7	4/23	39	74	11,200	6,320	33	22.9	10.7
4DI78	4/11	4/12	9	78	3,820	3,460	33	60.2	30.9
1GI86	4/12	4/16	26	35	287	250	35	115	48.2
2SH81	4/19	4/24	41	56	17,100	12,300	63	2,350	1,320
1SH84	4/20	5/4	72	57	175	46.2	64	499	129
3MF81	4/26	5/2	79	96	2,470	341	98	13,700	2,310
2KE72	4/28	4/30	12	83	5,510	3,460	83	484	463
2MF86	5/2	5/18	101	98	388	58.9	100	939	74.8
2MF85	5/3	5/11	58	79	1,330	661	71	108	37.5
5TK79	5/17	5/20	19	47	115	57.6	53	303	152
4MF81	5/20	5/24	75	89	278	37.8	100	3,070	491
1CH83	5/21	5/28	58	26	38.1	19.8	91	336	51.3
2PO85	5/22	6/2	83	37	84.2	16.5	64	58.7	9.8
2DA82	5/22	5/29	41	80	271	75.4	78	58.5	13.1
3SH81	5/23	5/28	42	33	51.5	20.3	86	1,920	466

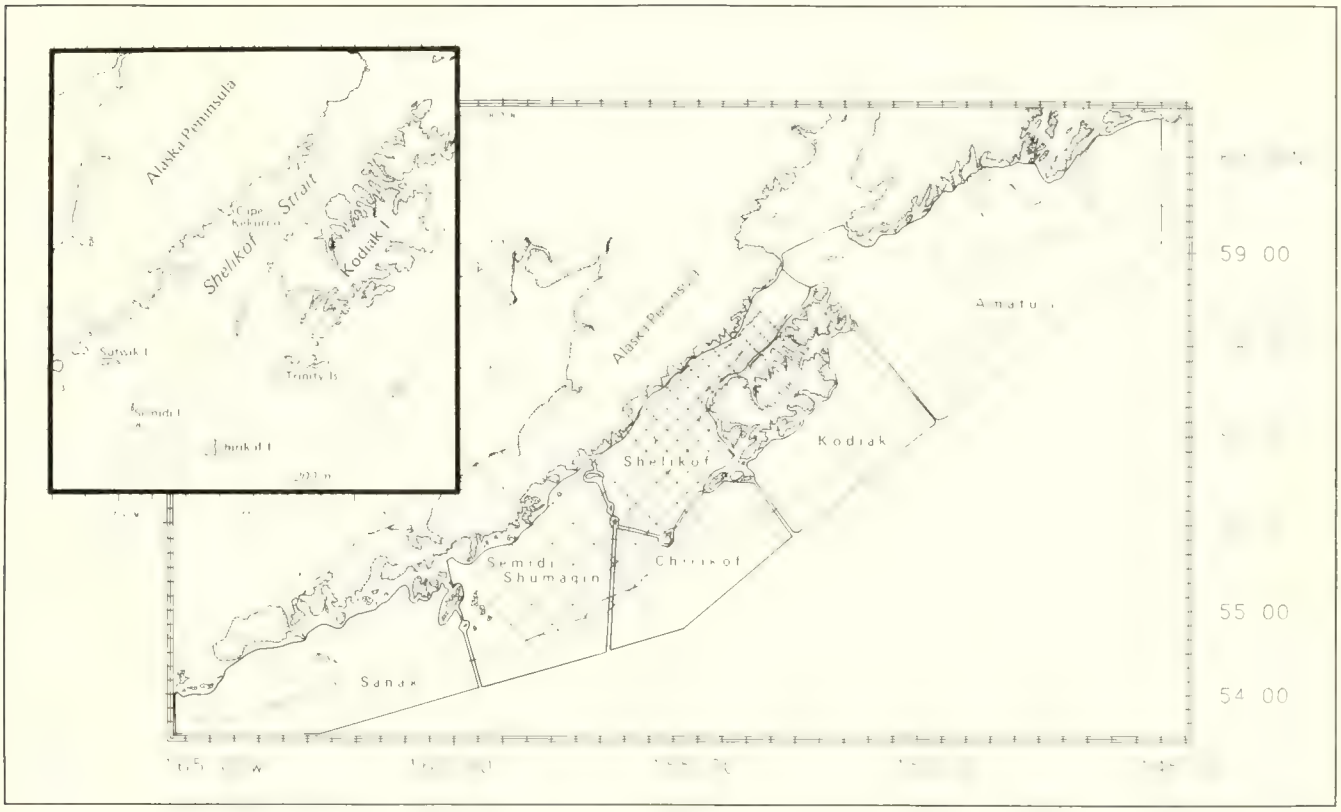

Figure 1

Gulf of Alaska showing the six strata used to analyze distribution of walleye pollock eggs and larvae. Gridded area was used in detailed analyses of the Shelikof Strait region.

The 32 cruises were conducted for a variety of purposes, so not all station patterns are ideal for the present analysis. Some results from these cruises have been reported elsewhere (Bates and Clark 1983, Dunn et al. 1984, Kendall and Dunn 1985, Bates 1987, Kendall et al. 1987). Although several ships were used, standard MARMAP oblique tows with 60-cm bongo nets (Smith and Richardson 1977) were conducted at all stations, with two exceptions: smaller bongo nets (20 cm) were used in 1984 aboard the NOAA ship *Chapman* and in April 1985 aboard the *Miller Freeman*. Mesh size was generally 505 μm, although 333-μm mesh was used aboard the NOAA Ship *Miller Freeman* in 1985 and 1986. On most cruises, sampling was conducted to a maximum depth of 200 m, as water depth permitted, but on the *Miller Freeman* in 1985 and 1986 sampling was conducted to within about 10 m of the bottom. Data collected from flowmeters in the mouth of the nets and bathykymograph records (for most tows) allowed us to determine the maximum depth and volume of water filtered for each tow. More details of the conduct of these cruises are found in Dunn and Rugen (1989).

Samples were preserved at sea in a 5% buffered formalin/seawater solution and returned to shore for processing. All fish eggs and larvae were then sorted from the samples, identified, counted, and the larvae were measured (mm standard length, SL): total sample when larvae numbered fewer than 50, or a random subsample of at least 50 when more than 50 larvae were in a sample. In each sample, developmental stages were determined for 100 randomly selected walleye pollock eggs according to the scheme of Matarese (Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070, unpubl. manuscr.) (see Kendall and Kim 1989). Egg development data were then grouped into the six age groups used by Kendall and Kim (1989). Numbers of eggs and larvae in the tows were standardized to numbers per 10-m^2 sea surface by calculating the volume of water filtered during the tow and dividing this number by the maximum depth of the tow.

Since most tows were taken to a maximum depth of 200 m, and substantial numbers of eggs occurred below this depth, we adjusted catches of eggs, based on data in Kendall and Kim (1989), to account for eggs below

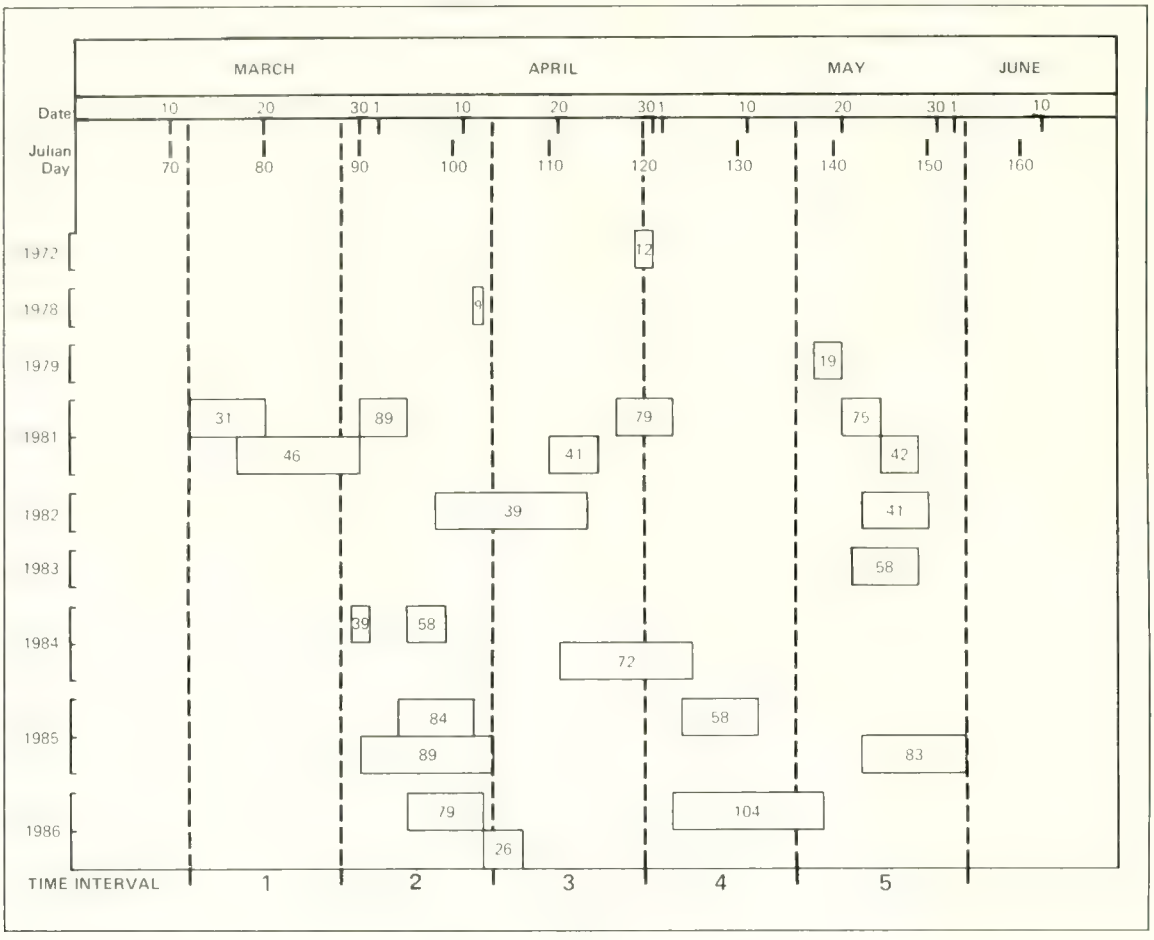

Figure 2

Cruise periods and time intervals used to analyze the distribution of walleye pollock eggs and larvae in Shelikof Strait. Numbers of tows are shown in blocks indicating cruise times.

the sampling depth. The percent of eggs that are expected to occur in the depth interval (A,B) is given by:

$$P_{A,B} = (0.06883) \cdot [\exp(0.02913 \cdot B) - \exp(0.02913 \cdot A)]$$

where $P_{A,B}$ = percent of eggs in depth interval (A,B); A = upper limit of depth interval, $\geqslant 40$ m; and B = lower limit of depth interval, $\leqslant 250$ m.

We assumed that no eggs occur at depths shallower than 40 m or deeper than 250 m. The adjustment was made by multiplying the catch per 10 m^2 by the ratio of the theoretical percentage of eggs that occur between 40 m and the bottom depth or 250 m (whichever is shallower) to the theoretical percentage of eggs that occur between 40 m and the maximum tow depth:

$$\text{Correction factor} = \frac{P_{40,\ \text{bottom depth or 250}}}{P_{40,\ \text{max. tow depth}}}.$$

In order to compare walleye pollock egg and larval catches at time of maximum abundance in various parts of the western Gulf of Alaska, we divided the gulf into six strata and examined egg and larval catches for each stratum (Fig. 1). For years in which more than one stratum was sampled (and at least three stations were sampled in a stratum), we used catches of eggs during April and catches of larvae from 16 May to 8 June for that year. For these cases, we calculated an area-weighted mean abundance (Sette-Ahlstrom method [see Appendix 1]) and percent contribution for each stratum.

For detailed analysis of the Shelikof Strait area, only those stations from Shelikof Strait to the Shumagin Islands were considered (see Fig. 1). Since the major spawning of walleye pollock in the western Gulf of Alaska occurs in Shelikof Strait in early spring (as we will show later), only cruises conducted in March through early June were considered in the detailed analysis of Shelikof Strait. In order to establish the

general pattern of occurrence of eggs and larvae as the season progressed, this time period was divided into five intervals (12–28 March, 29 March–13 April, 14–29 April, 30 April–15 May, and 16 May–2 June), and samples collected during each interval were grouped for analysis regardless of cruise or year (Fig. 2). Intervals of a 16-18 day duration were chosen because the egg incubation period is about this duration at ambient temperatures, and larvae would grow about 3 mm in this interval (at an observed growth rate of about 0.2 mm per day [Kendall et al. 1987]). Thus eggs or larvae within a 3-mm length increment from each time interval can be considered a cohort when comparing their distribution with that of adjacent time intervals.

Similarly, since sampling patterns and positions were different for each cruise, the Shelikof Strait area was divided into a number of sectors, and the samples that were collected in each time interval and each geographic sector were grouped so they could be analyzed regardless of cruise or year. The grid of sectors was laid out with axes parallel and perpendicular to the axis of Shelikof Strait (Fig. 1). Within Shelikof Strait proper, where heaviest concentrations of stations and abundances of eggs and larvae occurred, the sectors were 10×10 miles (18.5×18.5 km); southwest of this area the sectors were 20×20 miles (37×37 km).

The geographic distributions of walleye pollock eggs and larvae were summarized by mapping their centroids of distribution (see Appendix 2). Centroids were computed for total walleye pollock eggs and larvae by time interval regardless of year, and by egg age-group and 3-mm larval length-interval (3.0–5.9, 6.0–8.9, 9.0–11.9, 12.0–14.9, 15.0–17.9 mm SL). The centroid can be considered the center of mass of the distribution and is computed as the weighted mean location of the sectors, where the weights are the estimated total number of eggs or larvae for each sector (Koslow et al. 1985):

$$\text{Centroid} = (\bar{X}, \bar{Y})$$

$$\text{where } \bar{X} = \frac{\sum_i N_i \cdot X_i}{\sum_i N_i},$$

$$\bar{Y} = \frac{\sum_i N_i \cdot Y_i}{\sum_i N_i},$$

N_i = estimated total number of pollock in sector i

$$= \frac{A_i \cdot \sum_j N_{ij}}{n_i},$$

A_i = area of sector i (in units of 10 m^2)

N_{ij} = number of pollock per 10 m^2 for sample j in sector i,

n_i = number of samples in sector i,

X_i = center position of sector i in the east-west axis

$$= \frac{\sum_j N_{ij} \cdot X_{ij}}{\sum_j N_{ij}},$$

X_{ij} = position of sample j in sector i in the east-west axis,

Y_i = center position of sector i in the north-south axis

$$= \frac{\sum_j N_{ij} \cdot Y_{ij}}{\sum_j N_{ij}},$$

and Y_{ij} = position of sample j in sector i in the north-south axis.

The distribution was further analyzed by rotating the X and Y axes so that one axis was in the direction of the greatest geographic range of walleye pollock eggs or larvae in the study area. This axis is called the principal axis. The second axis is orthogonal to the principal axis.

An ellipse was drawn around the centroid that is one standard deviation away from the centroid along the rotated axes. The ellipse is defined as having the center at $(\bar{X}, \bar{Y})$ and the major axis parallel to the principal axis. The major and minor axes are each two standard deviations long. The ellipse is the two-dimensional analogue of a mean and standard error bars; it shows the center and the orientation of the animal's distribution in space and the amount of dispersion about the center. If the distibution of animals in space follows a bivariate normal distribution, then the ellipse is a 40% confidence contour.

Total abundance in the Shelikof Strait area was estimated for eggs and larvae for each time interval. Total abundances were also estimated for the six egg age-groups and the five larval length-increments for each time interval. The sectors were treated as strata to correct for the higher density of samples in areas of high egg and larval abundances. Not all sectors were sampled in each time interval, so the estimate of total abundance was adjusted to the total area. This was accomplished by grouping the sectors into two regions, (one included all the 10×10 mile sectors, and the other included all the 20×20 mile sectors), estimating a stratified mean density for each region, then multiply-

Table 3

Abundance of walleye pollock eggs and larvae in Shelikof Strait by time interval. Totals are expanded to total area of all sectors: (5.556×10^{11} m^2).

Time interval	Dates	Eggs			Larvae			No. sectors with samples
		Total (10^{12})	%	SD (10^{12})	Total (10^{12})	%	SD (10^{12})	
1	12–28 Mar.	0.710	1	0.0314	<0.001	0	<0.001	48
2	29 Mar.–13 Apr.	89.6	67	10.0	0.236	1	0.0385	68
3	14–29 Apr.	38.9	29	1.69	21.1	66	2.01	64
4	30 Apr.–15 May	2.91	2	0.198	5.32	17	1.24	67
5	16 Mar.–2 June	0.681	1	0.0427	5.09	16	0.515	74

ing the density by the total area of the region (Jessen 1978).

$$N = \sum_h A_h \cdot \bar{N}_h$$

where N = estimate of total abundance,
A_h = area of region h (in units of 10 m^2)
$\bar{N}_h$ = mean density in region h (number/10 m^2)

$$= \frac{\sum_i A_{hi} \cdot \bar{N}_{hi}}{\sum_i A_{hi}},$$

A_{hi} = area of sector i in region h (in units of 10 m^2)
$\bar{N}_{hi}$ = mean density in sector i in region h (number/10 m^2)

$$= \frac{\sum_j N_{hij}}{n_{hi}},$$

N_{hij} = number/10 m^2 in sample j in sector i in region h,
and n_{hi} = number of samples in sector i in region h.

The estimate of variance was adjusted to correct for sectors with one or no sample because a minimum of two samples are required to estimate variance for each sector (see Appendix 3).

$$\text{Var } N = \sum_i A_i^2 \cdot \text{Var } \bar{N}_i$$

where

$$\text{Var } \bar{N}_h = \frac{\sum_{i_+} A_{i_+}^2 \cdot \text{Var } \bar{N}_{i_+}}{A_h^2} \cdot \left[1 + \frac{\sum_{i_0} A_{i_0}^2}{\left(\sum_{i_+} A_{i_+}\right)^2}\right]$$

i_+ refers to sectors with at least two samples,
i_0 refers to sectors with one or zero samples,

and

$$\text{Var } \bar{N}_{hi_+} = \frac{\sum_j (N_{hi_+j} - \bar{N}_{hi_+})^2}{(n_{hi_+} - 1) \cdot n_{hi_+}}.$$

Results

General features of egg and larval distribution

Season of occurrence Of the 696 tows taken during the surveys from 1972 to 1979, 91 contained walleye pollock eggs and 76 contained larvae (Table 1). Between 28 March and 24 May, 205 tows were taken (29% of the total) and these included 82 and 75% of the tows containing walleye pollock eggs and larvae, respectively. A few of the tows taken between October and March also contained eggs, and the 88 tows in June and July accounted for an additional 20% of those containing larvae. From these results it appears that nearly all walleye pollock spawning and the egg and larval period in the Gulf of Alaska occurs in April and May (Table 2). Limited numbers of eggs are spawned earlier than this, and some larvae are available to plankton sampling after this.

Among the five time intervals between 12 March and 2 June established to investigate occurrences of eggs and larvae in the Shelikof Strait area, the second time interval (29 March to 13 April) accounted for 67% of the eggs, and the third time interval (14 to 29 April) accounted for 66% of the larvae (Table 3). The third time interval accounted for 29% of the eggs, and the fourth and fifth intervals accounted for 17 and 16% of the larvae, respectively. These results indicate that spawning in Shelikof Strait occurs mainly in early April, and that the larvae resulting from this spawning are present in the area in decreasing numbers into June.

Areas of occurrence Comparing the catches of walleye pollock eggs from April and larvae from 16 May to 8 June from the six strata, 89% of the eggs and 45%

Table 4

Abundance estimates ($\times 10^{10}$) of walleye pollock eggs and larvae in six strata of the western Gulf of Alaska. The top number is the number of stations sampled, and the bottom number is the number of eggs or larvae.

Year	Amatuli	Kodiak	Shelikof	Chirikof	Semidis-Shumagin	Sanak
Eggs (April)						
1981		15	104	13	16	
	[32.7]*	1.16	1670	102	1.60	[57.9]
1982		12	14	11	24	20
	[47.2]	1.24	907	99.0	21.6	48.2
1984	73	3	88	23	28	
	29.0	1.61	2240	0.510	0.744	[19.0]
1985	23	18	160	20	5	
	28.8	2.74	1220	177	0.434	[54.1]
1986	45	15	82	17	22	30
	11.3	2.47	635	13.5	13.1	88.3
Mean no. eggs	29.8	1.84	1330	78.4	7.50	53.5
Percent	1.98	0.122	88.6	5.20	0.498	3.55
Larvae (16 May–8 June)						
1979	11	13	8	9	10	7
	0.0409	0.00	38.4	0.0432	0.196	0.520
1981		11	93	13	15	
	[24.2]	0.0181	99.7	27.9	42.6	[10.4]
1982		4	15	13	23	6
	[4.80]	2.37	1.14	1.13	3.39	0.997
1985	40	3	49	23	30	29
	55.7	0.807	5.06	0.892	0.181	2.00
Mean no. larvae	21.2	0.798	36.1	7.50	11.6	3.47
Percent	26.3	0.990	44.7	9.30	14.4	4.30

*No data were available for abundance estimates in brackets; these values were predicted using a technique from analysis of variance for estimating missing data in a randomized block experiment (Cochran and Cox 1957), where the strata were considered as treatments, the years as blocks, and observed abundance estimates were log transformed.

of the larvae occurred in the Shelikof stratum (Table 4). The next most important stratum for eggs was Chirikof, where 5.2% occurred. The Amatuli stratum contained 26% of the larval catch, and the Semidis-Shumagin stratum contained 14%. Larval catches in the Amatuli stratum were based mainly on sampling done in 1985, a year in which larval occurrences in Shelikof Strait were dissimilar to all other years sampled (see later).

Distribution of eggs in Shelikof Strait

All ages Throughout the five time intervals, most sectors with high abundances of walleye pollock eggs were in Shelikof Strait proper (Fig. 3). The geographic pattern of abundance varied little among the time intervals. Most eggs were found near Cape Kekurnoi during the second time interval, although they were somewhat south of there during all other time intervals. Relatively few eggs occurred southwest of a line between Sutwik and Chirikof Islands.

The centroid for the first time interval was located off the southwest end of Kodiak Island (Fig. 4). In the second time interval, when most (67%) of the eggs were collected, the centroid was midway between Kodiak Island and the Alaska Peninsula, off Cape Kekurnoi. This is the area of maximum spawning as indicated by fishery catches and hydroacoustic surveys of adults (Alton 1987, Nelson and Nunnallee 1987). The centroid position from the first time interval is in an area where adults seem to congregate shortly before their ultimate move to the Cape Kekurnoi area. The size of the ellipses increased somewhat from the second through fifth time intervals, particularly in the along-strait direction,

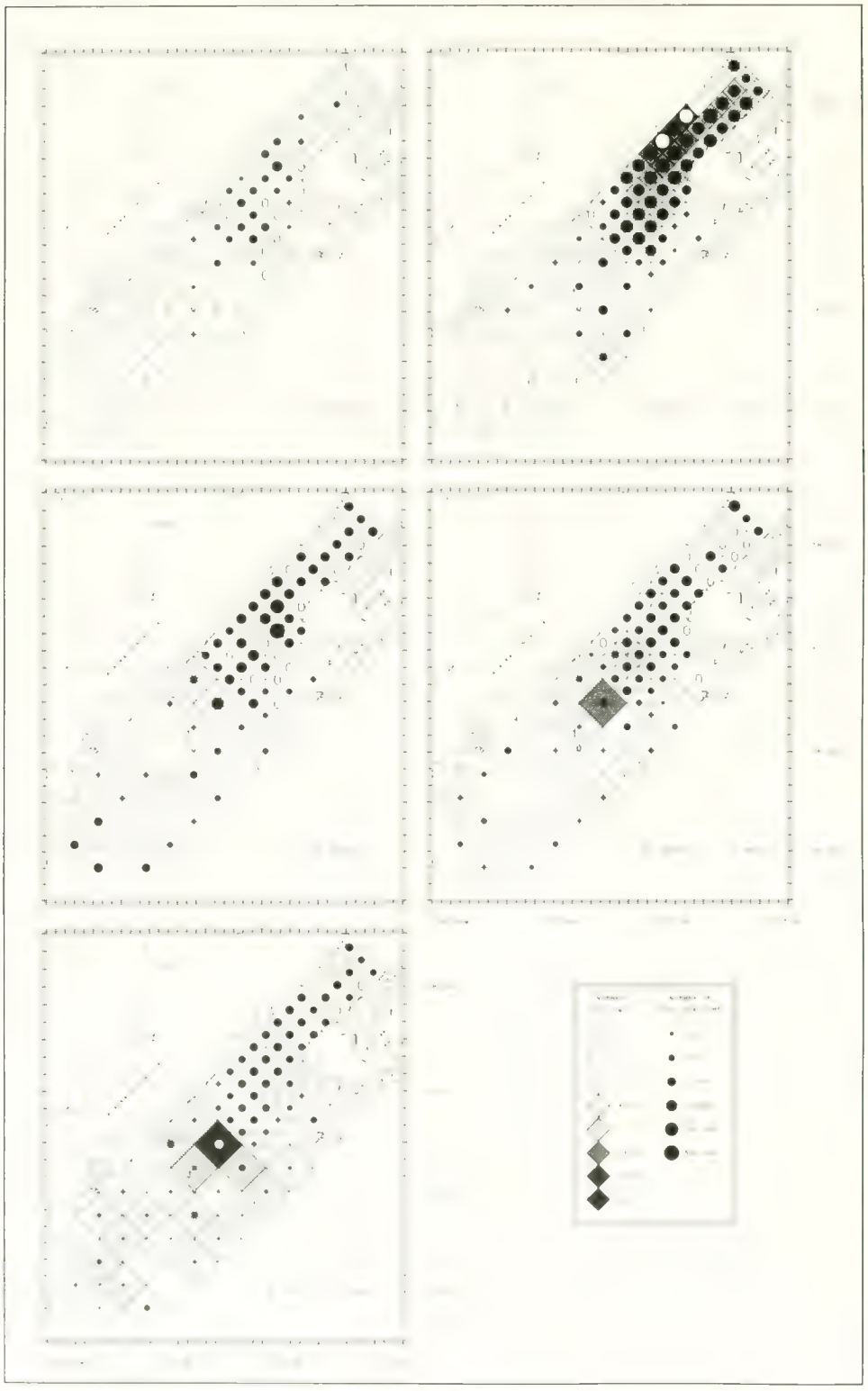

Figure 3
Distribution of walleye pollock eggs sampled in Shelikof Strait by time interval.

presumably indicating that more dispersed spawning occurs later in the season. Little change in spawning area through the season is indicated from the positions of the centroids. The centroids from the first, third, and fifth time intervals are essentially in the same location, whereas those from the second and fourth time intervals are further northeast, but in virtually the same locations. The sizes and positions of the ellipses

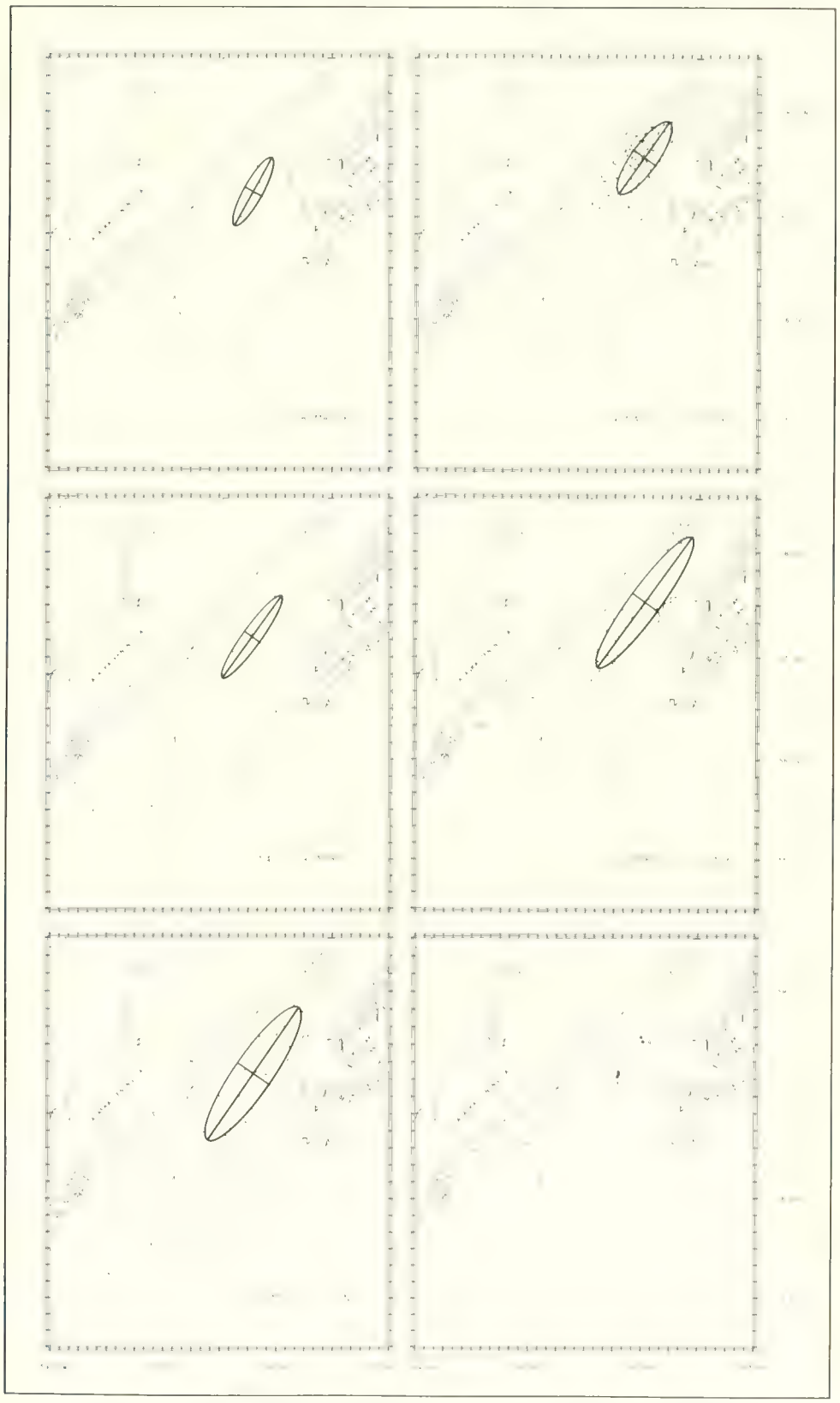

Figure 4

Centroids and associated ellipses of the distribution of walleye pollock eggs in Shelikof Strait. Dots show station locations. Lower right panel shows centroids for all five time intervals.

Table 5

Abundance of walleye pollock eggs in Shelikof Strait ($\times 10^{12}$/day) by age group and time interval. Cumulative hours to the endpoint of development of each age group at 5°C are based on Kendall and Kim (1989).

			Age group					
Time interval	Dates	Hours	1 23.0	2 70.5	3 114.5	4 166.5	5 226.5	6 316.5
1	12–28 Mar.		0.101	0.154	0.0558	0.0255	0.0152	0.0302
2	29 Mar.–13 Apr.		20.4	11.8	12.4	4.62	4.34	0.828
3	14–29 Apr.		1.23	3.07	2.75	1.93	4.75	2.81
4	30 Apr.–15 May		0.331	0.252	0.253	0.225	0.204	0.168
5	16 May–2 June		0.0502	0.0577	0.0636	0.0408	0.0503	0.0502

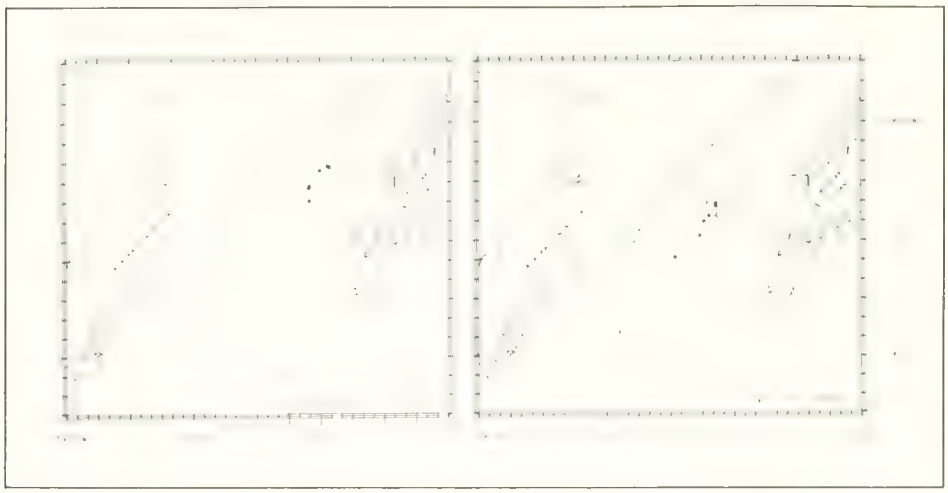

Figure 5

Centroids of walleye pollock egg distributions in Shelikof Strait by age group (see Table 5) during time intervals 2 (29 Mar.–13 Apr.) and 3 (14–29 Apr.).

reflect the extent of intra- and interannual variations in geographic patterns of distribution; and since the ellipses overlap each other, it appears that there is little variation in occurrences of the eggs through the season or among years. It should be noted, however, that the first time interval was sampled only in 1981; at least 5 years were sampled for all other time intervals.

By age group The trend in abundances over the various age groups of eggs varies with the time interval (Table 5). The young ages (groups 1–3) are much more abundant than the older ages (groups 4–6) in time intervals 1 and 2. This is due to the combined effects of mortality reducing the number of older eggs, and an increasing spawning rate producing young eggs at a higher rate than the older eggs were produced. During time intervals 3, 4, and 5, the abundances of young and old eggs are nearly equal. This is probably due to a declining spawning rate producing fewer young eggs; additionally the mortality rate might be lower than during time intervals 1 and 2.

Centroids of eggs by age group for the five time intervals indicated that in most cases random events and sampling error may have masked patterns of changes in spawning distribution and advection and dispersion of the eggs. The ellipses around the centroids of the six age groups generally overlapped one other within a time interval. It appears that distribution of spawning has more influence on distribution of eggs than advection, even though the eggs have a 2-week incubation period. Only the centroids of the six age groups of eggs for the second and third time intervals, when most eggs occurred, were analyzed (Fig. 5). The locations of centroids from the second time interval show that eggs in age groups 4–6 are close to one other and located south of eggs in age groups 1–3. This demonstrates that spawning during this interval may occur in two distinct but nearby areas. Spawning in the southern area would take place earlier than in the northern area, as indicated by the location of the centroid of all egg ages from the first time interval (Fig. 4). During the third time interval, the distribution of ages is the opposite of the pattern seen in the second time interval, with the older eggs located to the north of the younger eggs. This pattern indicates that the spawning adults were moving to the south during this time interval.

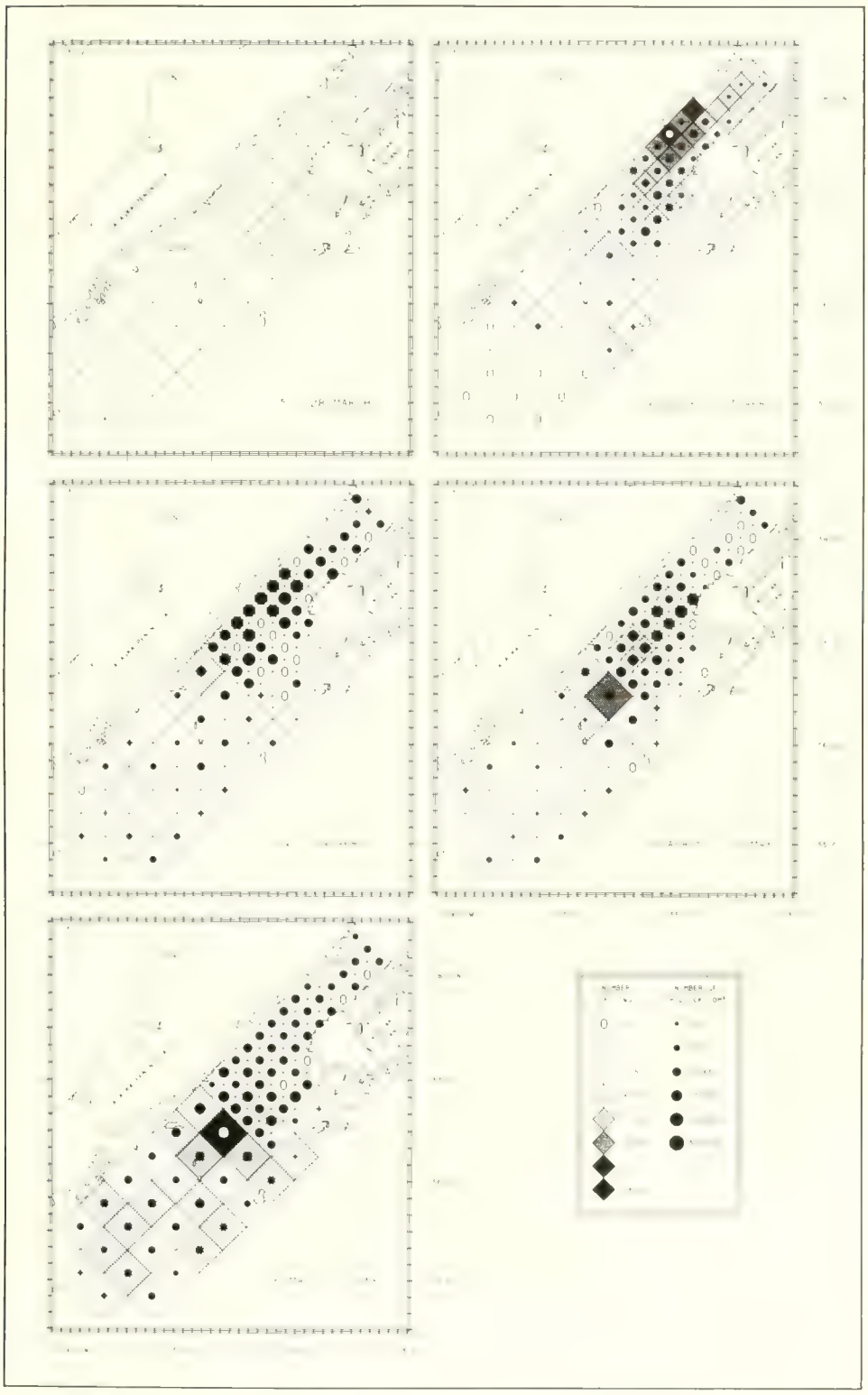

Figure 6
Distribution of walleye pollock larvae sampled in Shelikof Strait by time interval.

Distribution of larvae in Shelikof Strait

All lengths A single walleye pollock larva was found in the southwest corner of the study area during the first time interval (Fig. 6). By the second time interval, low numbers of larvae were found in most sectors in Shelikof Strait proper. Toward the southern end of the strait, they were mainly in the center of the strait, over the deep trough. A few sectors southwest of a line

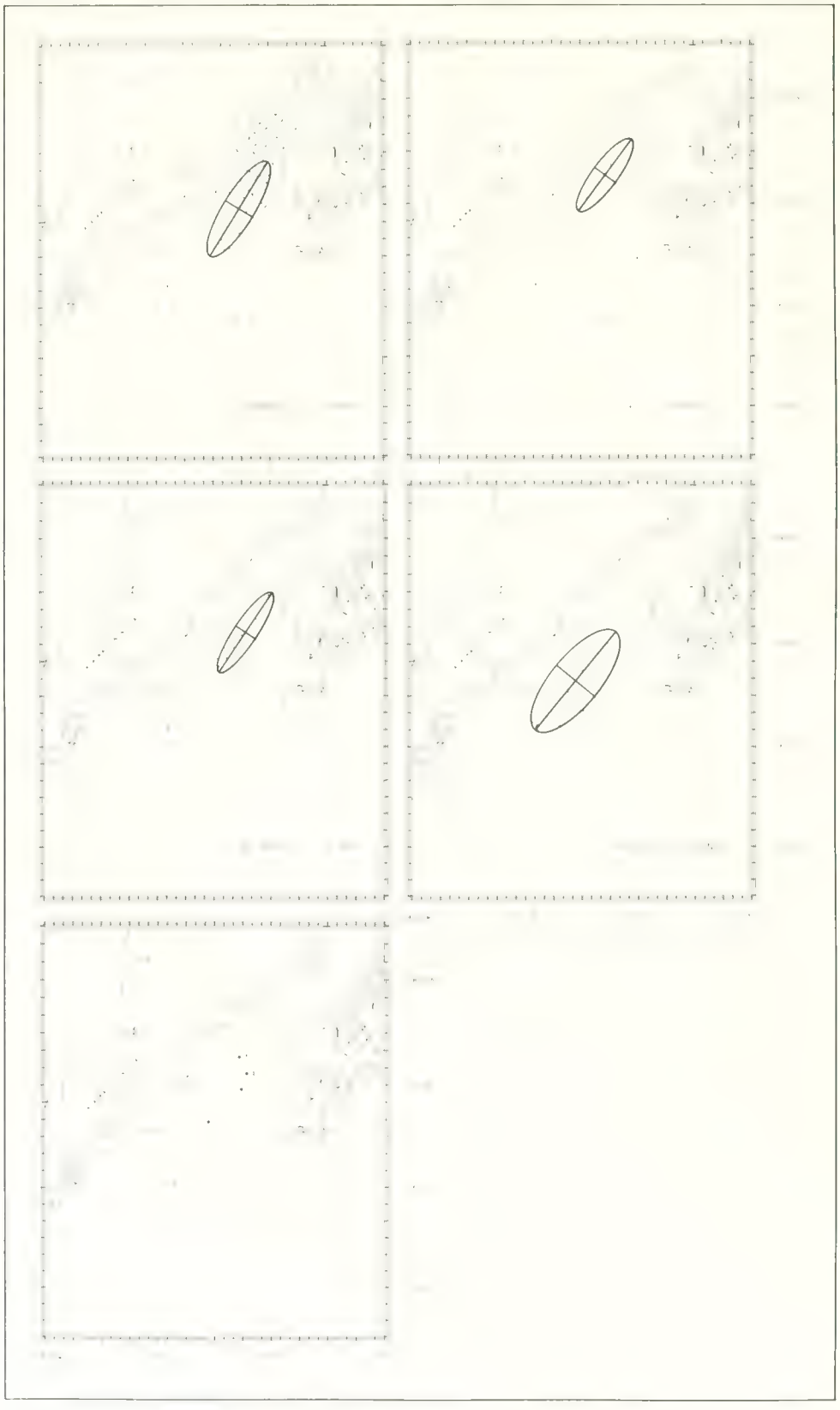

Figure 7

Centroids and associated ellipses of the distribution of walleye pollock larvae in Shelikof Strait. Dots show station locations. Lower panel shows centroids for second through fifth time intervals.

between Sutwik and Chirikof Islands had a few larvae. During the third time interval most sectors in Shelikof Strait proper contained large numbers of larvae. The larvae seemed to be most abundant along the Alaska Peninsula. South of Sutwik Island, most of the sectors contained a few larvae, with most larvae tending to occur in sectors along the deep trough and along the continental shelf margin. In the fourth time interval larvae were mainly in lower Shelikof Strait south to Chirikof Island. They were more abundant in the center of the strait over the deep trough than along the Alaska Peninsula. Larvae were present in nearly all sectors during the fifth time interval, and they were more widespread and relatively more abundant south of Sutwik Island than previously. Sectors with highest concentrations of larvae were between the south end of Kodiak Island and Chirikof Island.

Centroids of the larval distributions by time interval represent the results of spawning locations and advection and mortality of the eggs and larvae (Fig. 7). During the second time interval, the centroid of the larval distribution was over the deep trough between the Trinity Islands and the Alaska Peninsula, slightly south of the centroid of eggs during the previous time interval. The location of this larval centroid probably largely reflects advection of larvae from the eggs sampled in the previous time interval. These few larvae are not apparent in later time intervals, probably because their numbers are overwhelmed by larvae produced from the more intense later spawning near Cape Kekurnoi. The centroid of larvae during the third time interval was in the center of the strait between Cape Kekurnoi and Wide Bay. This is north of the larval centroid, but southwest of the egg centroid, from the previous time interval. Samples from the second time interval accounted for most of the eggs, whereas samples from the third time interval accounted for most of the larvae. The larvae collected in the third time interval primarily resulted from the eggs observed in the second time interval. The difference in location of the egg centroid from the second time interval and the larval centroid from the third time interval is probably largely due to advection to the southwest of eggs and larvae between these intervals. The larval centroid from the fourth time interval was displaced slightly to the south of the larval centroid from the third time interval. The sizes of the ellipses from these two time intervals were essentially equal, indicating that physical diffusive processes were balanced by biological processes of recruitment and mortality and physical processes counteracting dispersal. The larval centroid from the fifth time interval was displaced to the southwest from that of the fourth time interval, and the ellipse was considerably larger. The shape of the ellipse indicated that the larvae were more dispersed in both the along- and across-strait directions than previously. Based on the low numbers of eggs collected after the second time interval, the larval centroids from the fourth and fifth time intervals largely reflect displacement of eggs and larvae first seen as eggs during the second time interval.

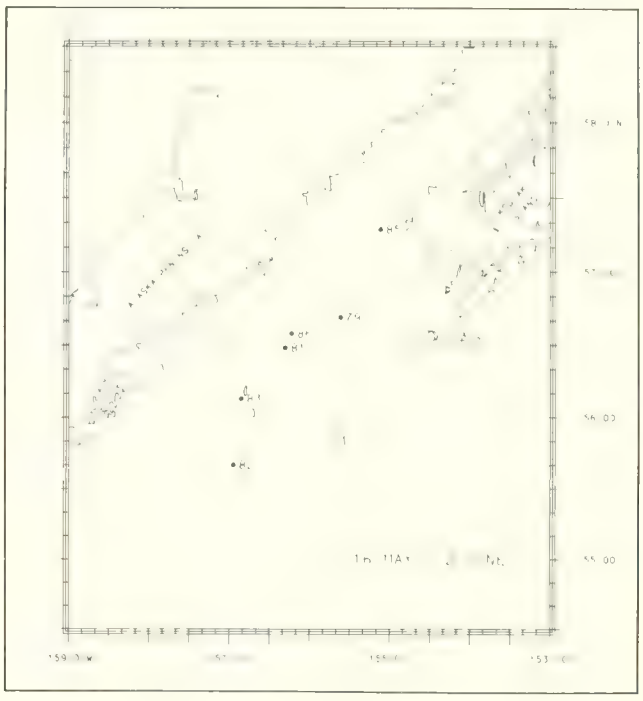

Figure 8
Centroids of walleye pollock larval distributions in Shelikof Strait during the fifth time interval (16 May–2 June), 1979–86.

Interval 5 by year The fifth time interval evinced considerable variation in the location of the larval centroids among the years sampled (Fig. 8). The centroid of larvae in 1985 was off the westernmost coast of Kodiak Island. The ellipse from 1985 was quite elongate in its along-strait axis due to the occurrence of larvae further north in Shelikof Strait than seen in any other year sampled. The centroids from 1979, 1981, and 1986 were close to one another over the trough between Sutwik and Chirikof Islands. In 1983, the centroid was in the Semidi Islands, and in 1982 it was further south, between Chirikof Island and the Alaska Peninsula. The centroid from 1985 was 290 km northeast of the centroid from 1982.

Larval lengths A plot of weighted mean length of larvae versus weighted mean sampling date* for each

*Weighted mean sampling date = $\bar{D}$, where

$$\bar{D} = \frac{\sum N_i D_i}{\sum N_i}.$$

N_i = number/10 m^2 in sample i, and
D_i = day of year when sample i was taken.

cruise permits a comparison among years, and provides an estimate of the increase in length of fish in the population with time (Fig. 9). The mean length of larvae in the population at a particular time results from a combination of time since spawning and individual growth, as well as the effects of mortality. Older larvae will have been subjected to mortality for longer periods than younger larvae, so the change in length of larvae in the population should be less than individual growth rate. In 1978, 1979, and 1983, only one cruise sampled larvae. However, in 1981 and 1985, five and four cruises, respectively, sampled larvae. Altogether, 20 cruises were available to assess larval-population length increase.

Before the third time interval, little increase in the length of larvae in the population or variation among years in size of larvae was evident. The mean lengths were 3–6 mm. Larvae at the end of April were smallest in 1981 and largest in 1985. After the middle of May, the larval population length seemed to increase at a fairly uniform and linear rate through the end of May. In 1981, 1982, and 1985, larvae in late May were between 7 and 9 mm. In 1983, however, larvae were over 10 mm in late May. Excluding the larval lengths from 1983, the length data from the third through fifth time intervals fit the straight line of

$$\text{length (mm SL)} = -9.60 + 0.122 \cdot \text{day of year},$$

with $r^2 = 89.7$. Thus the population increased in length at a rate of about 0.12 mm/day. Based on analysis of larval otolith daily growth increments, individual growth in 1983 was 0.2 mm/day (Kendall et al. 1987).

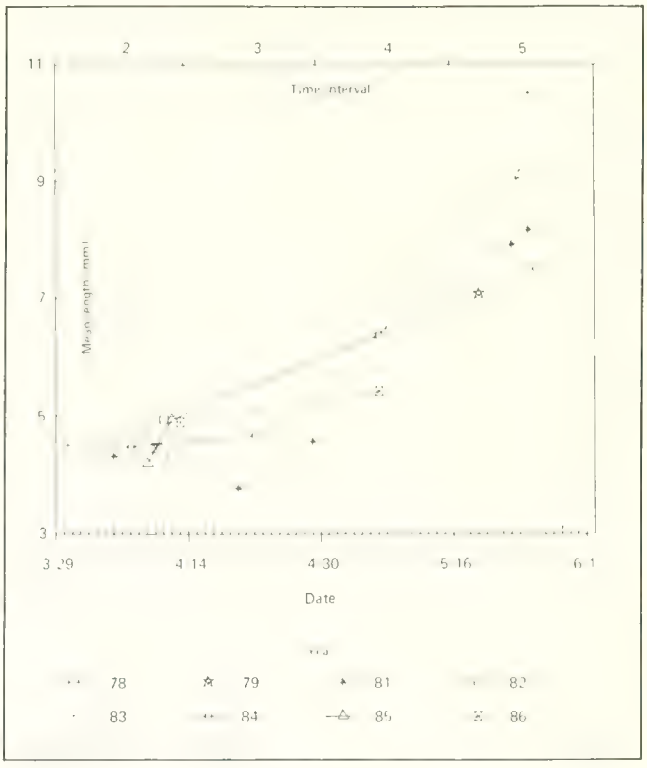

Figure 9
Lengths of walleye pollock larvae by sampling date and year.

Distribution of cohorts of eggs and larvae in Shelikof Strait

The five time intervals of 16–18 days were about equal to the incubation period of the eggs, and the larvae grew about 3 mm (~0.17 mm/day) during each time interval, after hatching at 3–4 mm. Thus eggs from one time interval were assumed to be the 3–6 mm larvae observed in the following time interval, the 6–9 mm larvae in the time interval after that, and so on. Under this assumption three cohorts (1–3) were established, based on eggs from the first, second, and third time intervals, regardless of year, in order to examine the geographic displacement of the eggs and larvae during development (Table 6). Changes in abundance with time in the cohorts is influenced by differences among years in sampling and overall population abundances, which prevent estimation of mortality rates.

Eggs in the first cohort, those from the first time interval, were slightly northeast of larvae in this cohort, which were represented by 3–6 mm larvae from the second time interval (Fig. 10). The centroid of larvae that were 3–6 mm long in the second time interval was in the southern end of Shelikof Strait, midway between the southern end of Kodiak Island and the Alaska Peninsula. In the third time interval the first cohort (6–9 mm larvae) was centered further to the southwest, just north of a line between Sutwik and Chirikof Islands. In the fourth time interval the 9–12 mm larvae were centered near the position of the centroid of the 3–6 mm larvae in the second time interval. The ellipse for these larvae was quite elongate (Table 6), indicating considerable dispersion on the along-strait axis. This pattern reflects differences in the distribution of this size larvae among years, particularly in the abundance of these larvae in the northern part of Shelikof Strait in 1985. The centroid of the 12–15 mm larvae from the fifth time interval is positioned in the Semidi Islands, and the ellipse is broadened in the across-strait dimension compared with the previous ones. Thus, excluding the fourth time interval, which was influenced by the aberrant pattern of 1985, the first cohort of eggs and larvae appears to have been advected to the southwest in the center of the strait from the southern end of Kodiak Island to the Semidi Islands between early April and late May.

Table 6

Abundance ($\times 10^{12}$) and dimensions of ellipses (of three cohorts) of walleye pollock eggs and larvae in Shelikof Strait by time interval and 3-mm length increment for larvae. Cohorts are indicated by the diagonal numbered boxes. Areas in km^2; axes in km.

Time interval	Dates		Cohort	Eggs	Larvae: Length increments (mm SL) 3–6	6–9	9–12	12–15	15–18
			1						
1	12–28 Mar.	Abundance		0.710	<0.001	0.000	0.000	0.000	0.000
		Area		1340					
		Major axis		83					
		Minor axis		21					
			2						
2	29 Mar.–13 Apr.	Abundance		89.6	0.231	0.004	0.000	0.000	0.000
		Area		2080	3400				
		Major axis		93	132				
		Minor axis		28	33				
			3						
3	14–29 Apr.	Abundance		38.9	19.7	0.204	0.001	0.000	0.000
		Area		1710	2440	1570			
		Major axis		108	104	95			
		Minor axis		20	30	21			
4	30 Apr.–15 May	Abundance		2.91	4.79	0.512	0.012	0.000	0.000
		Area			2030	4920	6310		
		Major axis			108	160	230		
		Minor axis			24	39	35		
5	16 May–2 June	Abundance		0.681	0.275	3.40	1.27	0.137	0.004
		Area				4780	9220	8910	
		Major axis				117	183	166	
		Minor axis				52	64	68	

The second cohort, represented by eggs from the second time interval and 3–6 mm larvae from the third time interval, resulted from the period of heaviest spawning activity. Most of the eggs and larvae collected were in this cohort. The centroid of the eggs of this cohort, in the second time interval, was in the middle of Shelikof Strait, off Cape Kekurnoi (Fig. 10). During the third time interval, the centroid of larvae of the second cohort (3–6 mm long) was located east of Wide Bay, southwest of the centroid of eggs of this cohort. In the fourth time interval, 6–9 mm larvae were further to the southwest, off the south end of Kodiak Island. By the fifth time interval, 9–12 mm larvae were near a line between Sutwik and Chirikof Islands. The ellipses for this cohort of eggs and larvae expanded between each successive time interval (Table 6).

The centroid of eggs of the third cohort was found in the center of Shelikof Strait, off Wide Bay (Fig. 10). The centroid of this cohort as 3–6 mm larvae (during the fourth time interval) was positioned at the southern end of Shelikof Strait, closer to Kodiak Island than to the Alaska Peninsula which was slightly south of where the eggs were. In the fifth time interval the centroid of this cohort as 6–9 mm larvae was between Sutwik Island and the Trinity Islands.

Figure 10
Centroids of three cohorts of walleye pollock egg and larval distributions in Shelikof Strait. Labels beside dots indicate stage (egg) or length increment, with time interval in parentheses.

Discussion

As we compiled data for analysis, we made several assumptions which may have affected our results. Most of the tows used to describe egg distributions did not exceed a maximum depth of 200 m and, therefore, a correction factor was applied to account for eggs in deeper parts of the water column. Our key assumption for this correction was that the depth distribution of eggs found in Shelikof Strait in 1985 and 1986 was applicable throughout the study area and for all years examined. The validity of this assumption needs to be verified by determining geographic and interannual variability in depth distribution and bouyancy of eggs. Specific gravity and depth distribution of the eggs change with development (Kendall and Kim 1989), but these changes were not accounted for in our analysis.

In many of the analyses, there was an implicit assumption that samples were drawn randomly from within a sector or stratum. Some of what appears to be random variability in the data may be features of distribution on a scale too fine for our analyses. In combining data from various years with slightly different sampling times and station patterns, small-scale interannual differences may have been blended. Effects of different sampling intensities among the years may have interacted with changes in overall abundance of eggs and larvae, so that patterns in low adundance years may have been overwhelmed by patterns from high abundance years. However, aside from the unusual spatial distribution of larvae in 1985, and the large size of larvae in late May 1983, timing and geographic areas of occurrence of eggs and larvae seemed quite consistent among years.

Knowledge of the distribution of eggs and larvae of walleye pollock in the Gulf of Alaska has increased dramatically in recent years. The larvae could not be separated from those of Pacific cod *Gadus macrocephalus* prior to studies of Matarese et al. (1981). Kendall and Dunn (1985) summarized knowledge of ichthyo-

plankton, including walleye pollock in the Gulf of Alaska based on sampling prior to 1980. Very little sampling had been done before 1977, when a series of cruises was conducted mainly southeast of Kodiak Island. Eggs were found mainly nearshore in spring, and to a lesser extent in fall. Larvae were found in spring and summer throughout the shelf and slope area sampled. The spawning concentration in the Shelikof Strait was discovered inadvertantly in 1980. The mean number of eggs and larvae per 10 m^2 in cruises reported by Kendall and Dunn (1985) did not exceed 40 and 228 respectively, whereas we found mean numbers per cruise as high as 177,000 for eggs and 13,700 larvae in Shelikof Strait (Table 2).

Based on the patterns of distribution elucidated here, several topics for future work are indicated. By comparing distributions of cohorts of eggs and larvae, we inferred advection rates and directions. The reasonableness of these drift patterns needs to be investigated based on the physical oceanography of the area.

Although these results show that most spawning occurs in Shelikof Strait, evidence of some spawning south of Chirikof Island was observed. Surveys of adults producing the eggs in this area need to be conducted so that the importance of the area can be evaluated. The source of the eggs and larvae found in the Amatuli area and the northern part of Shelikof Strait in 1985 also needs to be established.

The cruises available for this study were made only through early June. By this time the larvae had drifted a considerable distance southwest of the spawning area and grown to about 8–11 mm. The distribution of larvae later in spring and summer is virtually unknown. To understand recruitment in this population, the larvae need to be followed through summer to find the location of their nursery area. Such information is a necessary prerequisite to studies of factors contributing to survival throughout the planktonic stages of walleye pollock.

During the years of study here, the adult spawning biomass of walleye pollock in Shelikof Strait declined from $3.77 \cdot 10^6$ mt in 1981 to $0.62 \cdot 10^6$ mt in 1986 (Nelson and Nunnallee 1987). The planktonic egg data from these years can be analyzed to see how closely they reflect this decrease in spawning biomass. Based on the analysis here, a model of seasonal and geographic egg production could be developed that would allow extrapolation of expected egg catches when sampling did not cover the entire area of their occurrences.

Given the interannually consistent patterns of egg distribution in Shelikof Strait described here, there is a reasonable opportunity to establish egg and larval mortality rates based on changes in population abundance during April and May. The timing of changes in mortality could be determined, and differences in mortality rates among years could be investigated. This can lead to studies of the environmental and biological causes of mortality and how these vary during the season and interannually. Knowledge of these variations in mortality rates is critical to an understanding of recruitment patterns in this population.

Summary

Based on analysis of walleye pollock egg and larval distributions in 1,929 MARMAP bongo tows taken on 32 cruises in the northern Gulf of Alaska from 1972 to 1986, we made the following conclusions:

1 Most eggs occur in April, and larvae occur in late April through May.
2 Most eggs and larvae result from spawning in Shelikof Strait near Cape Kekurnoi.
3 Little difference in geographic distribution of eggs was seen through the season or among the years sampled.
4 Larvae occurred progressively to the southwest of the area of egg occurrence, as the larvae developed through the season.
5 Larval population averaged from 4.2 to 4.9 mm in mid April, and reached 7.5 to 9.1 mm by the end of May, except in 1983 when the population averaged 10.5 mm at the end of May.
6 Considerable variation in distribution of larvae was seen by late May among the years sampled, indicating differences in amount of advection.

Acknowledgments

Sample collection and processing, as well as the data entry and editing that went into producing this publication, required contributions of persons too numerous to mention; however, without them we could not have considered undertaking this project. Suffice it to say that the environment that walleye pollock find suitable for spawning is often extremely inhospitable to those on ships collecting their eggs and larvae, and we appreciate the efforts of all involved. Most samples were sorted and fish eggs and larvae identified, counted, and staged (eggs) or measured (larvae) at the Polish Plankton Sorting Center under the direction of Dr. Leonard Ejsymont, whose diligence in overcoming the many problems associated with such demanding work, as well as the challenges of a cooperative program between two countries, is gratefully acknowledged. Many people at NWAFC assisted in processing egg and larval samples, but we particularly want to thank Ann Matarese, Beverly Vinter, and Deborah Blood. Jay Clark and Richard Bates at NWAFC made the data

required ready for analysis and Bates performed some of the analyses. Dr. Suam Kim, University of Washington and NWAFC, advised us on depth adjustments of egg catches and on the use of centroids for our analysis. Dr. Paul Smith, Southwest Fisheries Center, and Dr. Don Gunderson, University of Washington, reviewed and made valuable comments on an earlier draft.

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Appendix 1

The mean density for each cruise or stratum was estimated by the Sette-Ahlstrom method:

$$\bar{N} = \frac{\sum_{i}^{n} A_i \cdot N_i}{A} \qquad \text{(Richardson 1981)}$$

where $\bar{N}$ = mean number per 10 m^2,
A_i = area represented by station i (in units of 10 m^2),
N_i = number per 10 m^2 in sample i,

$A = \sum_{i}^{n} A_i$ = total area of survey or strata (in units of 10 m^2), and

n = the number of A_is in A.

Total abundance was estimated by $N = A \cdot \bar{N}$,

where N = total number in survey or strata.

The areas A_i are polygons as described in Richardson (1981). The variance of N was estimated using methods from probability sampling theory (Jessen 1978). The A_is may be different sizes, and one sampling unit (the water below 10 m^2 of surface area) is sampled in each A_i. Thus, the probability that a particular sampling unit is included in the survey depends on which A_i the sampling unit occurs.

$$P_{ij} = \frac{1}{A_i \cdot n}$$

where P_{ij} = probability that sampling unit j in A_i is selected in the survey.

This leads to the same estimate of $\bar{N}$ as given in Richardson (1981):

$$N_i = \frac{1}{A \cdot n} \cdot \sum_{i}^{n} \frac{N_i}{P_i} \qquad \text{(Jessen 1978, eq. 8.15)}$$

$$= \frac{1}{A \cdot n} \cdot \sum_{i}^{n} N_i \cdot A_i \cdot n$$

$$= \frac{\sum_{i}^{n} A_i \cdot N_i}{A}.$$

The estimate of the variance of mean density is

$$\text{Vâr } \bar{N} = \frac{1}{A^2 \cdot n \cdot (n-1)} \cdot \sum_{i}^{n} \left(\frac{N_i}{P_i} - \frac{1}{n} \cdot \sum_{i}^{n} \frac{N_i}{P_i} \right)^2 \qquad \text{(Jessen 1978, eq. 8.17)}$$

$$= \frac{1}{A^2 \cdot n \cdot (n-1)} \cdot \sum_{i}^{n} \left(N_i \cdot A \cdot n - \frac{1}{n} \cdot \sum_{i}^{n} N_i \cdot A_i \cdot n \right)^2$$

$$= \frac{n}{A^2 \cdot (n-1)} \cdot \sum_{i}^{n} \left(N_i \cdot A_i - \frac{A}{n} \cdot \bar{N} \right)^2.$$

And the variance of the total abundance is estimated by

$$\widehat{\mathrm{Var}}\,N = A^2 \cdot \widehat{\mathrm{Var}}\,\bar{N}.$$

Appendix 2

The centroid is simply the weighted bivariate mean of the sampled locations of the eggs or larvae. Its estimated value depends on where the samples were taken and the size of the catch. If the samples are not evenly or randomly spaced over the study area, then $(\bar{X}, \bar{Y})$ will be biased towards those areas with the highest sample density. This bias can be avoided by either grouping the individual samples into strata (sectors) as done here, or by modifying the computation of $(\bar{X}, \bar{Y})$ to account for unequal sample density as was done to estimate the mean and variance for the Sette-Ahlstrom method (see Appendix 1).

The rotation of the X and Y axes is specified by the slope of the principle axis, b_1 (Sokal and Rohlf 1981):

$$b_1 = \frac{\mathrm{Cov}(X,Y)}{\lambda_1 - \mathrm{Var}(X)},$$

where $$\mathrm{Cov}(X,Y) = \frac{\sum_i N_i \cdot (X_i - \bar{X}) \cdot (Y_i - \bar{Y})}{\left(\sum_i N_i\right) - 1},$$

$$\lambda_1 = \text{the first latent root of the variance-covariance matrix of } X \text{ and } Y,$$

$$= 0.5 \cdot \left[\mathrm{Var}(X) + \mathrm{Var}(Y) + \sqrt{(\mathrm{Var}(X) + \mathrm{Var}(Y))^2 - 4 \cdot (\mathrm{Var}(X) \cdot \mathrm{Var}(Y) - \mathrm{Cov}(X,Y)^2)}\right],$$

$$\mathrm{Var}(X) = \frac{\sum_i N_i \cdot (X_i - \bar{X})^2}{\left(\sum_i N_i\right) - 1}, \text{ and}$$

$$\mathrm{Var}(Y) = \frac{\sum_i N_i \cdot (Y_i - \bar{Y})^2}{\left(\sum_i N_i\right) - 1}.$$

The ellipse about the centroid is specified by the standard deviations along the rotated axes. The standard deviation in the direction of the major axis is equal to λ_1 as defined above. The standard deviation in the direction of the minor axis is equal to λ_2, which is the second latent root of the variance-covariance matrix of X and Y:

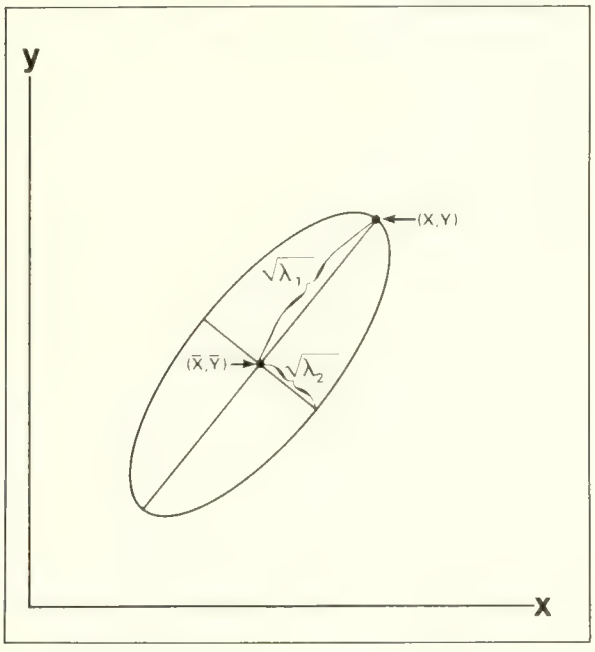
$$\lambda_2 = \mathrm{Var}(X) + \mathrm{Var}(Y) - \lambda_1.$$

Sokal and Rohlf (1981, box 15.5) give a formula for an ellipse of this shape but of a different size:

$$\mathrm{Var}(Y) \cdot (X - \bar{X})^2 - 2\,\mathrm{Cov}(X,Y) \cdot (Y - \bar{Y}) \cdot (X - \bar{X}) + \mathrm{Var}(X) \cdot (Y - \bar{Y})^2 = C.$$

By setting C to the appropriate value, this formula can define the ellipse as specified above and shown in Appendix Figure 1. The value for C is derived from the formula for the point (X, Y) given in Sokal and Rohlf (1981, box 15.5):

$$X = \bar{X} + \sqrt{\frac{C}{\lambda_1 \cdot (1 + b_1^2)}} \qquad \text{and} \qquad Y = \bar{Y} + b_1 \cdot (X - \bar{X}).$$



Appendix Figure 1
Ellipse with the center at $(\bar{X}, \bar{Y})$ and the major and minor axes each two standard deviations long.

The criterion that the length of the major axis is $2 \cdot \lambda_1$ implies that

$$\lambda_1 = (X - \bar{X})^2 + (Y - \bar{Y})^2$$

based on the Pythagorean theorem. By substituting in the formulas for X and Y given above, this formula can be rewritten as

$$\lambda_1 = \frac{C}{\lambda_2 \cdot (1 + b_1^2)} + \frac{b_1^2 \cdot C}{\lambda_2 \cdot (1 + b_1^2)} = \frac{C}{\lambda_2},$$

solving for C:

$$C = \lambda_1 \cdot \lambda_2.$$

Thus the equation for the ellipse is

$$\mathrm{Var}(Y) \cdot (X - X)^2 - 2\,\mathrm{Cov}(X,Y) \cdot (Y - Y) \cdot (X - X) + \mathrm{Var}(X) \cdot (Y - Y)^2 = \lambda_1 \cdot \lambda_2.$$

This ellipse is estimated by substituting the estimated values for the variances, covariance, means, and latent roots.

No distributional assumptions are needed to estimate the centroid, the slope of the principal axis, or the shape of the ellipse. The centroid is the standard measure of central tendency and is valid as long as the stations represent a valid sample of the survey area. The slope of the principal axis is defined by the line that minimizes the sum of the squared perpendicular distances between the data and the line. The size and shape of the ellipse are set by the variance of the data about the centroid. The ellipse is simply a two-dimensional version of a mean with standard error bars.

In the univariate case, the mean and standard error provide information about the location of the data's center of gravity and the amount of dispersion about that center, no matter what probability function the data come from (Shuster 1982). However, if the data are from a normal distribution, a confidence interval may be computed directly from the mean and standard error. If the data are from a bimodal or skewed distribution, the mean and standard error are still valid, but viewing the mean with standard error bars can give the false impression that the data are distributed symmetrically about the mean, when in fact the confidence interval would be asymmetrical if the data are asymmetrical.

Similarly, caution should be employed in interpreting the centroid and ellipse. No matter what probability function describes the spatial distribution of the eggs and larvae, the centroid is the measure of central tendency and the ellipse shows the orientation of the data and the amount of dispersion along the two axes. However, the ellipse can only be considered a contour or an "equal frequency ellipse" about the centroid if the data are from

a bivariate normal distribution. In this case the proportion of the population expected to be enclosed by the ellipse may be estimated as follows.

Sokal and Rohlf (1981) state that if

$$C = \frac{\lambda_1 \cdot \lambda_2 \cdot (n-1) \cdot 2}{(n-2)} \cdot F_{\alpha[2,n-2]}$$

then the ellipse is expected to enclose $100 \cdot (1-\alpha)\%$ of the observations.

The α that corresponds to the ellipse used in this study can be determined by finding the value for α such that

$$\lambda_1 \cdot \lambda_2 = C = \frac{\lambda_1 \cdot \lambda_2 \cdot (n-1) \cdot 2}{(n-2)} \cdot F_{\alpha[2,n-2]},$$

which can be rewritten as

$$F_{\alpha[2,n-2]} = \frac{(n-2)}{(n-1) \cdot 2}.$$

If n is very large, then $(n-2)/(n-1)$ is close to 1 and

$$F_{\alpha[2,\infty]} \sim \frac{1}{2}$$

which corresponds to $\alpha = 0.6065$. Thus the ellipse is expected to enclose approximately 40% of the observations.

Appendix 3

The usual stratified estimate of variance is

$$\text{Vâr } \bar{N}_h = \frac{\sum_i A_{h_i}^2 \cdot \text{Vâr } \bar{N}_{h_i}}{A_h^2} \qquad \text{(Jessen 1978)}$$

which may be rewritten as

$$\text{Vâr } \bar{N}_h = \frac{\sum_{i_+} A_{h_{i_+}}^2 \cdot \text{Vâr } \bar{N}_{h_{i_+}} + \sum_{i_0} A_{h_{i_0}}^2 \cdot \text{Vâr } \bar{N}_{h_{i_0}}}{A_h^2}.$$

where i_+ refers to sectors with at least 2 samples, and i_0 refers to sectors with 1 or 0 samples.

There are no data to estimate Var $\bar{N}_{h_{i_0}}$ directly, so it is estimated with the average variance from sectors where there are at least two samples.

Let

$$\text{Vâr } \bar{N}_{h_{i_0}} = \frac{\sum_{i_+} A_{h_{i_+}}^2 \cdot \text{Vâr } \bar{N}_{h_{i_+}}}{\left(\sum_{i_+} A_{h_{i_+}}\right)^2}, \text{ for all } i_0.$$

This estimate of Var $N_{h_{i_0}}$ is substituted back into the formula estimating Var $\bar{N}_h$, giving

$$\text{Vâr } \bar{N}_h = \frac{\sum_{i_+} A_{h_{i_+}}^2 \cdot \text{Vâr } \bar{N}_{h_{i_+}} + \sum_{i_0} A_{h_{i_0}}^2 \cdot \dfrac{\sum_{i_+} A_{h_{i_+}}^2 \cdot \text{Vâr } N_{h_{i_+}}}{\left(\sum_{i_+} A_{h_{i_+}}\right)^2}}{A_h^2}$$

which simplifies to

$$\text{Vâr } \bar{N}_h = \frac{\sum_{i_+} A_{h_{i_+}}^2 \cdot \text{Vâr } \bar{N}_{h_{i_+}}}{A_h^2} \cdot \left(1 + \frac{\sum_{i_0} A_{h_{i_0}}^2}{\left(\sum_{i_+} A_{h_{i_+}}\right)^2}\right).$$

Abstract.– We investigated increment formation in sagittae of Atlantic menhaden *Brevoortia tyrannus* in laboratory experiments, and found that the age of individual larvae can be estimated within ±3 days over the first month of life using counts of growth increments. Sagittae were first observed during embryonic development. The first prominent growth increment was formed at first feeding, and the frequency of increment formation of fed and starved larvae ranged from 0.86 to 0.98 increments per day thereafter. Starvation did not appear to systematically alter the periodicity of increment formation from one increment per day, although it consistently modified the width of growth increments among different age groups of larvae. Microstructural growth patterns in sagittae responded rapidly (days) to changes in feeding: larvae starved for 1–3 days formed narrow, poorly-defined increments compared with fed larvae that formed wide, well-defined increments. Standard length and estimated dry weight of larvae were related to sagittal radius by asymptotic and logistic functions, respectively. Sagittal radius of larvae was related to days after first feeding by a logistic function. Our results for Atlantic menhaden confirm the potential of otoliths in providing information about age, stressful events, and growth history of individual fish larvae.

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Effects of Starvation on the Frequency of Formation and Width of Growth Increments in Sagittae of Laboratory-Reared Atlantic Menhaden *Brevoortia tyrannus* Larvae

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Rates of growth and survival of young fish are hypothesized to affect the abundance of the incoming year-class (Lasker 1985, Rothschild 1986). Both biotic (e.g., prey resources) and abiotic (e.g., water temperature) factors have a direct effect on the growth and survival of freshwater and marine fish larvae. Microstructural growth patterns in otoliths of teleost fish may provide a record of environmental and physiological condition throughout the larval and juvenile stages and hence important information about processes regulating recruitment in fish (Pannella 1980, Houde 1987, Rice et al. 1987).

The examination of microstructural growth patterns in otoliths for making inferences about the ecology of young fishes has become a popular technique since Pannella (1971) postulated that annuli (yearly growth zones) consisted of growth increments formed on a daily basis. Subsequently, microstructural growth patterns have been used to estimate age and growth histories of fish (Methot and Kramer 1979, Penney and Evans 1985), infer the temperature chronology of larval and juvenile life stages (Radtke 1984, Gauldie et al. 1986), detect life history transitions (Brothers and McFarland 1981, Campana 1984a), and investigate patterns of recruitment and mortality (Crecco et al. 1983, Essig and Cole 1986) and stock identification (Mulligan et al. 1987).

Age validation studies of larval and juvenile fishes have shown that microstructural characteristics are species-specific and may be influenced by nutrition and/or environmental variables (Campana and Neilson 1985, Rice et al. 1985, Jones 1986). Fish larvae subjected to periods of stress (e.g., starvation) or cyclic environmental variables (e.g., diel fluctuations in water temperature) may have their increment deposition disrupted, resulting in apparent nondaily formation (Taubert and Coble 1977, Jones 1984, Neilson and Geen 1985). These results suggest that validation studies are necessary for a species before analysis of otolith microstructure can be used to age individuals in nature. Substantial errors may be incorporated into the analysis if daily increment formation is assumed but nondaily deposition occurs (Campana and Neilson 1985).

Few studies have assessed the effect of short-term starvation on the accuracy of age estimates and growth histories of the early life stages of fish derived from the analysis of otolith microstructure. This paper examines the reliability of sagittal microstructure of larval Atlantic menhaden to estimate age, detect stressful events, and infer the growth chronology of individual larvae. Two age groups of laboratory-reared larvae were subjected to short periods of starvation and optimal feeding conditions to determine the relationship between age, growth history, and microstructural growth patterns in sagittae.

The Atlantic menhaden is a commercially and ecologically important species along the Atlantic east coast (Reintjes 1969, Reish et al. 1985). Recruitment of this species has undergone marked fluctuations since monitoring of the fishery began in the 1940's (Ahrenholz et al. 1987). Investigations of the early life stages of Atlantic menhaden indicate that physical and biological factors operating during larval drift may influence the growth and survival and hence recruitment (Nelson et al. 1977, Checkley et al. 1988). Information derived from these laboratory experiments will serve as a basis for interpreting the microstructure of sagittal otoliths of Atlantic menhaden larvae collected in nature (Maillet 1988).

Methods

Spawning and rearing conditions

Fertilized eggs (henceforth called the "stock population") were obtained from an induced spawn of a captive stock (Hettler 1981, 1983) and placed into three circular tanks containing 60-L of filtered (20 μm) seawater. Eggs and larvae were incubated at 19°C (18.9 ± 0.1°C; $\bar{x} \pm$ SE) in lightly aerated, static water with overhead fluorescent lighting on a 12 L:12 D photoperiod. Salinity ranged from 29 to 33 g/kg. Furan II (7 mg/L, Aquarium Pharmaceuticals) was added to retard the growth of bacteria and fungi. During early development (first feeding to 12 days postfertilization), larvae were offered cultured algae *Nanochloris* spp., rotifers *Brachionus plicatilis*, and wild microzooplankton (70–250 μm size range) ad libitum. During later development, larvae were offered only wild microzooplankton. Dead larvae and settled plankton were removed every 1–3 days. Water level was maintained by removal of seawater each time food was added.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Experimental procedures

Eggs were sampled daily during development and preserved in 95% ethanol to investigate otolith formation in embryos. A total of 15 eggs were used in the analyses. To estimate the time to first increment formation and to test for subsequent daily increment formation, 10 to 15 larvae were sampled from the stock population at 3, 4, 5, 6, 7, 8, 11, 14, 25, 34, and 35 days postfertilization. The effect of starvation on the periodicity of increment formation was investigated by exposing two different age groups of larvae (13–20 days, and 28–36 days postfertilization) to short periods with no food. For each group, larvae of various sizes were randomly selected from the stock population and transferred to eight 10-L experimental tanks filled with 20-μm filtered seawater. Initial densities of larvae in experimental tanks were 5 larvae/L (13–20 days) and 4 larvae/L (28–36 days). Environmental conditions, including illumination, water temperature, salinity, and the use of Furan II, were identical to those of the stock tanks. Four experimental groups, consisting of (a) continuous feeding (controls), (b) 1-day starved, (c) 2-day starved, and (d) 3-day starved treatments, were randomly assigned to duplicate experimental tanks. Control larvae were fed wild microzooplankton ad libitum immediately after transfer; treatment larvae received food at the end of the respective starvation interval and were allowed to continue feeding for several days after this period.

All larvae sampled from the stock and experimental containers were first anesthetized with tricaine methanesulfonate (Cresent Research Chemical), measured for standard length (tip of upper jaw to end of notochord) to the nearest 0.1 mm, and then preserved in 95 % ethanol. Larvae were stored individually in 10-mL vials. The preservative was changed once after 48 hours to maintain sagittae in optimal condition.

Otolith preparation and analysis

Sagittae were examined within two months after preservation. The right sagitta was teased from the inner ear with minuten needles, cleaned of excess tissue, and mounted medial-side-up in Flo-Texx (Lerner Laboratories). Specimens were examined with transmitted light under a compound microscope fitted with a 100× objective and a video camera and monitor, thereby increasing the total magnification (monitor image/actual size) to 3600×. An electronic caliper was used to measure growth increments on the video monitor. This system allowed electronic enhancement of otolith images (e.g., contrast between the incremental and discontinuous zones).

Increment counts were made in triplicate on masked (i.e., of unknown origin) samples, to minimize bias, and

the mean calculated. If triplicate counts deviated by ± 3 increments or more, the specimen was excluded from further analysis. Five percent of the samples were thereby excluded. Another 16% of the specimens were excluded from the analysis because of our inability to resolve increments in some specimens and/or improper orientation for viewing specimens. Linear regressions of mean increment count on days after first feeding were computed for each experimental group. Student's t was used to determine whether increment formation is initiated at first feeding (i.e., regression intercept = 0) and growth increments are formed daily (i.e., slope = 1.0). Statistical power to detect a deviation of 0.1 from a slope of 1.0 at $p = 0.05$ level (two-sided test) was estimated for each linear regression (Rice 1987, Steel and Torrie 1980). Analysis of variance was used to test the homogeneity among all slopes.

The width of growth increments formed before, during, and after starvation was measured for 5–10 larvae from each experimental tank. Increment width was measured from the perimeter moving inward along the maximal radius, the inner end of the radius being defined as the center of the nucleus. This line was consistently the best for enumerating increments. To eliminate bias in measurement of increment width the focal plane was adjusted, if necessary, for the measurement of each increment. Increment width was averaged for each larva over each of the three treatment intervals (i.e., fed, starved, refed), except for the 1-day starved treatment during starvation. Analysis of covariance (ANOCOVA) was used to compare the mean width of growth increments between larvae from the control and treatment tanks during and after starvation (Steel and Torrie 1980). Since the duration of the starvation and recovery intervals varied with length of starvation, the ANOCOVA tested for differences in mean increment width between larvae from control and treatment tanks within intervals. The interval duration was identical between comparisons of mean increment width of larvae from the control and treatment tanks. Comparison of increment width between fed and starved larvae within intervals was necessary because of age-related trends in increment width. The covariate included in the ANOCOVA was mean increment width prior to the starvation and recovery intervals. The ANOCOVA took into account any differences in the width of growth increments of larvae allocated to the experimental tanks and provided a more accurate comparison between individuals from control and treatment groups.

The relationships between sagittal radius, standard length, estimated dry weight, and days after first feeding were also investigated. We pooled all of the larvae in the treatment groups (i.e., 1-, 2-, and 3-day starved larvae) for analysis, except that starved larvae were excluded when estimating the dry weight—otolith size relation since these measurements were not made directly on individual larvae. Sagittal radius was measured from the center of the nucleus to the perimeter along the maximal radius. Dry weight of individual larvae was estimated from a linear regression of log-transformed dry weight (DW, μg) on log-transformed standard length (SL, mm) : $\ln DW = -3.041 + 3.799 \ln SL$, $n = 195$, $r^2 = 0.95$. This equation was derived for laboratory-reared Atlantic menhaden larvae ranging in size from 5 to 25 mm (Checkley et al., ms in prep.). Linear and nonlinear regressions of standard length and estimated dry weight on sagittal radius, and sagittal radius on days after first feeding were compared to determine the best predictive models. Average growth rates (AVG, mm/day) of larvae for both age groups were estimated from first feeding (ff) to experiment termination by: $AVG = (SL - 4.7)/(\text{days after ff})$, where 4.7 is the average standard length (mm) at first feeding (Powell and Phonlor 1986).

Results

Increment description and larva growth rate

Sagittae were first observed during embryonic development and consisted of the dark and apparently proteinaceous primordium (Fig. 1). Examination of sagittae with the light microscope revealed that no growth increments were formed during this period. At hatching, the sagitta resembled a flattened spheroid or hemisphere with a mean radius of 4.8 ± 0.3 μm, $n = 15$. The first increment surrounding the primordium was typically characterized by a wide discontinuous zone and coincided with hatching. In some cases, 3–4 narrow, poorly defined increments were observed outside the first increment. Limited resolution of the light microscope did not always allow these increments to be resolved, counted, and/or measured. The first prominent increment in sagittae formed 3–4 days after hatching and coincided with the initiation of exogenous feeding. This prominent growth increment was used as the starting point for subsequent counts along the maximal radius.

Mean size at hatching for this laboratory population of Atlantic menhaden was 3.59 ± 0.22 mm SL, $n = 100$ (range 3.08–4.00 mm). The average growth rate of menhaden larvae from first feeding to experiment termination was 0.368 ± 0.006 mm/day (13–20 days) and 0.360 ± 0.004 mm/day (28–36 days). Size range for the two age groups examined was 6.4–13.0 mm and 10.3–20.0 mm SL. This rate of growth slightly exceeded the estimate of 0.32 mm/day based on data of Powell and Phonlor (1986) for Atlantic menhaden larvae reared at 20°C. Larvae did not metamorphose

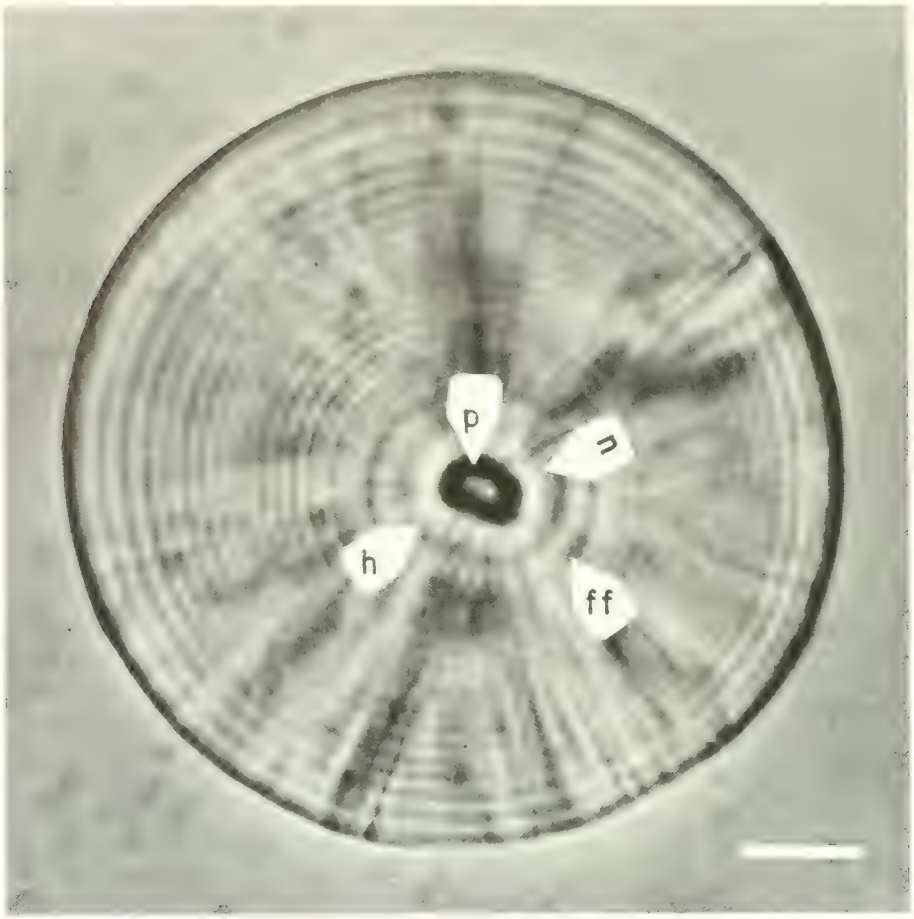

Figure 1
Light micrograph of sagittal otolith of a 22 day-old (postfertilization) laboratory-reared Atlantic menhaden larva showing 18 growth increments. The primordium (p) is delineated by an innermost protein-rich layer. The nucleus (n) is delineated by the first continuous growth increment surrounding the primordium. The first growth increment formed at hatching (h) is characterized by a thick protein-rich layer, and the first prominent growth increment is formed at first feeding (ff). Scale bar represents 10 μm.

in this experiment, but estimates in the literature indicate that wild Atlantic menhaden transform to the juvenile life stage at 25–30 mm (Lewis et al. 1972, Nelson et al. 1977).

Initiation and frequency of increment formation

The time to first increment formation and frequency of increment deposition were estimated from linear regressions of mean increment count on days after first feeding. The regression intercepts of larvae from the stock population and control and treatment groups were not significantly different from zero, except for the 1-day starved treatment, indicating that the first prominent increment is formed at or near the time of first feeding (Table 1).

Frequency of increment formation varied from 0.86 to 0.98 increments/day among experimental groups (Table 1, Fig. 2). There did not appear to be any systematic effect of starvation on frequency of increment formation. The rate of increment formation for both the control and 1-day starved treatments were significantly different from one increment/day, but the stock population, 2-, and 3-day starved treatments formed increments at a rate not significantly different from one increment per day. Computations of statistical power indicated low variability among the increment count—age regressions and provided additional confidence that growth increments are formed daily. The test for homogeneity of slopes indicated a significant difference between larvae from the control and pooled treatments ($p<0.05$, $n=108$). The difference between the estimated slopes for individuals from the control and 1-day starved treatment tanks accounted for this difference. The estimated pooled slope for the control and 2- and 3-day starved treatments was not significantly different in the test for homogeneity among slopes ($p>0.63$, $n=68$).

Response of increment width to changes in larva feeding

Since there were no significant differences in increment width between duplicate containers within different levels of treatments ($p>0.05$, ANOVA), measurements

Table 1

Least-squares regressions of mean increment count on days after first feeding (*ff*) of laboratory-reared Atlantic menhaden: Increment count = $a + b$ (days after *ff*). Asterisks denote significant deviations from the hypothesized values (H_0: $a = 0$, $b = 1.0$, Student's t: $^*p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$).

Experimental group	n	Intercept $a \pm$ SE	Slope $b \pm$ SE	r^2	95% CL[1]	Power[2]
Stock	79	-0.01 ± 0.11	0.98 ± 0.01	0.99	± 1.8	0.99
Control			*			
0-day starved	27	0.73 ± 0.63	0.92 ± 0.03	0.97	± 2.4	0.90
Treatments		***	***			
1-day starved	40	2.15 ± 0.39	0.86 ± 0.02	0.98	± 2.2	0.99
2-day starved	20	-0.19 ± 0.58	0.96 ± 0.03	0.98	± 2.4	0.91
3-day starved	22	-0.47 ± 0.74	0.94 ± 0.04	0.97	± 2.6	0.82

[1]95% confidence limits (CL) for estimating increment count of an individual larva from time of first feeding.
[2]Estimate of statistical power to detect a deviation of 0.1 from a slope of 1.0 at the $p = 0.05$ level.

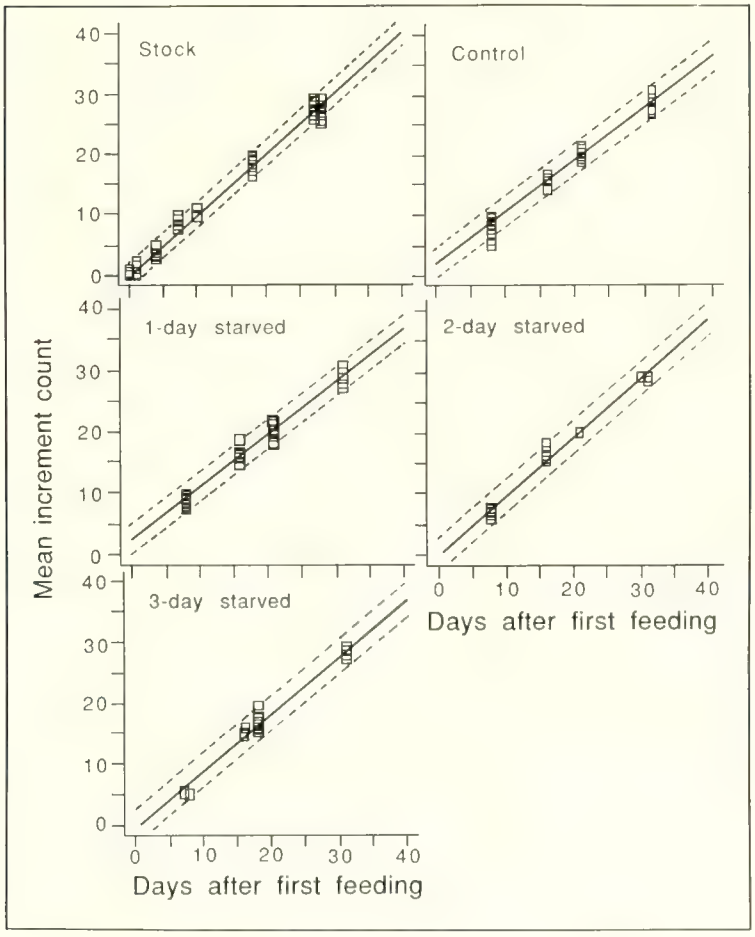

Figure 2

Least-squares regression (—) of increment count on days after first feeding and 95% confidence limits (----) for estimating mean increment count of an individual Atlantic menhaden larva. Some symbols represent more than one observation. Statistics are given in Table 1.

of increment width of larvae from duplicate control and treatment tanks were pooled. Prior to starvation, no significant differences ($p>0.05$) were observed in mean increment width between larvae from control and treatments except for the control and 3-day starved treatment in the older age class. The mean width of growth increments differed significantly ($p<0.05$) between fish from control and treatments during the respective periods of starvation and recovery (Fig. 3). The width of growth increments was significantly larger in fed compared with starved larvae. In general, the magnitude and significance of these differences

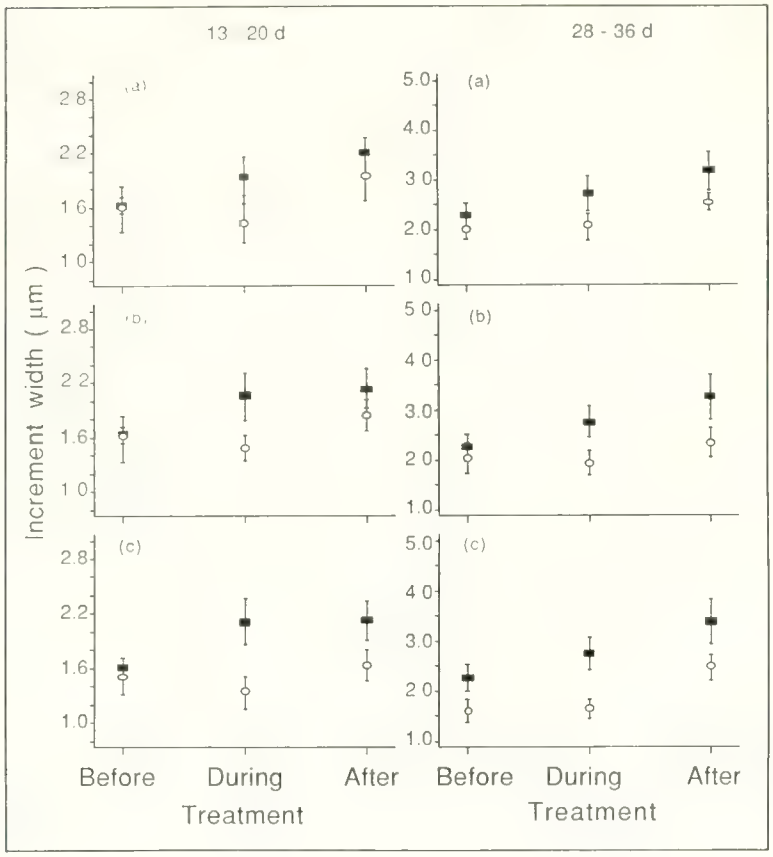

Figure 3
Mean increment width of Atlantic menhaden larvae from control (fed, ■) and treatment (1–3 day starved, O) tanks before, during, and after the respective starvation interval. (a) 1-day starved, (b) 2-day starved, and (c) 3-day starved larvae. Vertical bars represent standard errors.

increased with longer starvation, and both age classes of larvae responded similiarly to these stressful events. Starved larvae in both age classes displayed narrow [1.4 ± 0.1 µm, $n = 60$, (0.7–2.2 µm, range), 13–20 days; 1.8 ± 0.3 µm, $n = 63$, (1.0–3.2 µm), 28–36 days] poorly defined increments while control larvae exhibited wider [2.1 ± 0.2 µm, $n = 30$, (1.2–2.8 µm), 13–20 days; 2.7 ± 0.6 µm, $n = 57$, (1.3–4.6 µm), 28–36 days] well-defined increments during the starvation interval. After starvation, mean increment width of starved larvae in both age classes increased during the 3–6 day recovery interval (Fig. 3).

The results of the ANOCOVA, which adjusted for mean increment width prior to the initiation of starvation, indicated that mean increment width differed significantly ($p<0.05$) between individuals from control and treatment tanks during starvation in both age classes (Table 2). This result suggests that differences in mean increment width arose during the starvation interval and were not due to differences prior to this interval. However, during the recovery interval, no significant differences ($p>0.05$) were observed between larvae from control and treatment tanks when adjusted by the covariate. This result suggests that differences observed between individuals from control and treatments during the recovery interval were the result of differences formed during the starvation interval, and indicates that increment width of larval Atlantic menhaden responds rapidly to short-term variations in feeding.

Relationship between sagittal size and body size and sagittal size and age

Visual inspection of residuals for regressions of standard length and estimated dry weight on sagittal radius, and sagittal radius on days after first feeding, indicated that nonlinear models were superior to linear models in all cases. Asymptotic regressions of standard length on sagittal radius were fit separately for larvae from control and pooled treatments (Fig. 4a). The regressions were highly significant ($p<0.0001$) and residuals were distributed at random over the entire size range examined, indicating that the models fit the data well. The regression coefficients for fed larvae were slightly larger than for starved larvae. A logistic function was used to regress estimated dry weight on sagittal radius (Fig. 4b). Data were log-transformed to stabilize the variance and reduce the influence of larger values on the regression. Starved larvae were excluded from this relationship since dry weights were estimated from standard length. The regression was highly

Table 2

Comparison of least-squares means (adjusted for the covariate in the ANOCOVA) of increment width during and after starvation between control (fed) and treatment (starved) Atlantic menhaden larvae aged (a) 13–20 days, and (b) 28–36 days. N refers to the number of larvae examined, while n corresponds to the total number of observations of increment width from which the mean was calculated. Asterisks denote significant deviations between larvae from control and treatment tanks; * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

			Mean increment width (μm)	
Experimental group	N		During treatment $\bar{x}\pm$SE (n)	After treatment $\bar{x}\pm$SE (n)
(a)				
Control	10	*	1.89±0.13 (10)	2.08±0.12 (69)
1-day starved	10		1.48±0.13 (10)	2.01±0.12 (70)
Control	10	**	2.05±0.11 (20)	2.00±0.10 (59)
2-day starved	10		1.49±0.11 (20)	1.89±0.10 (60)
Control	10	***	2.12±0.12 (30)	1.94±0.11 (49)
3-day starved	10		1.33±0.12 (30)	1.81±0.11 (50)
(b)				
Control	19	*	2.63±0.09 (19)	2.97±0.12 (109)
1-day starved	19		2.28±0.12 (13)	2.73±0.14 (84)
Control	19	***	2.68±0.10 (38)	2.73±0.14 (90)
2-day starved	18		2.03±0.14 (12)	2.97±0.19 (42)
Control	19	**	2.53±0.10 (57)	2.94±0.10 (71)
3-day starved	10		2.03±0.14 (30)	3.32±0.16 (38)

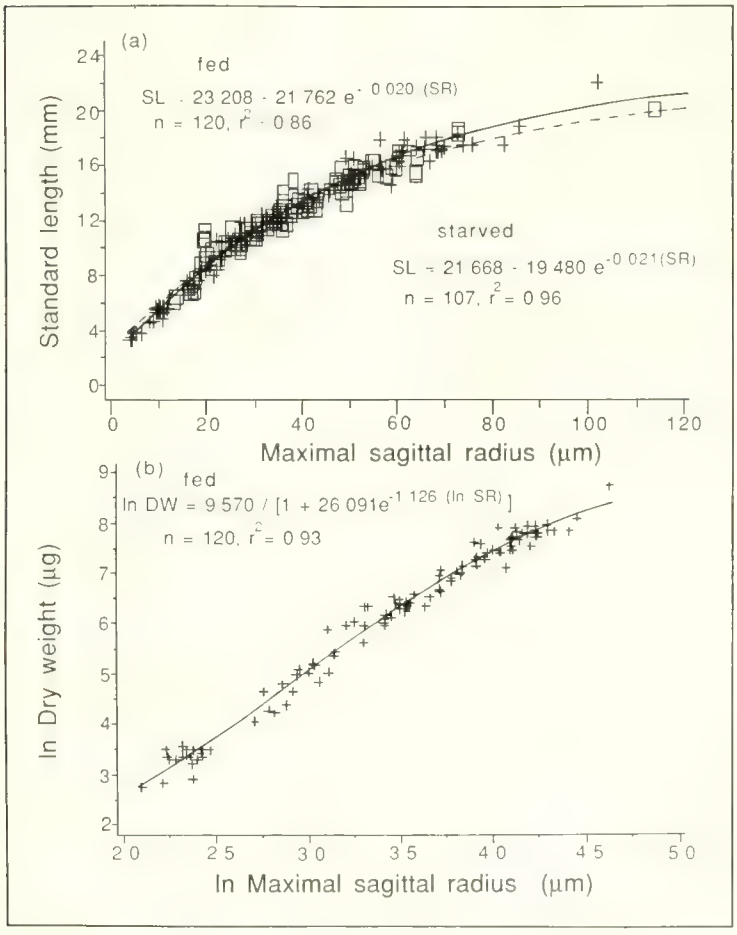

Figure 4

(a) Nonlinear regressions of standard length (SL) on sagittal radius (SR) of Atlantic menhaden larvae from control (solid line, +) and treatment (1–3 day starved, broken line, □) tanks. (b) Nonlinear regression of log-transformed estimated dry weight (DW) on log-transformed sagittal radius (SR) for control (+) larvae only. Model coefficients and other descriptive statistics are also presented. Some symbols represent more than one observation.

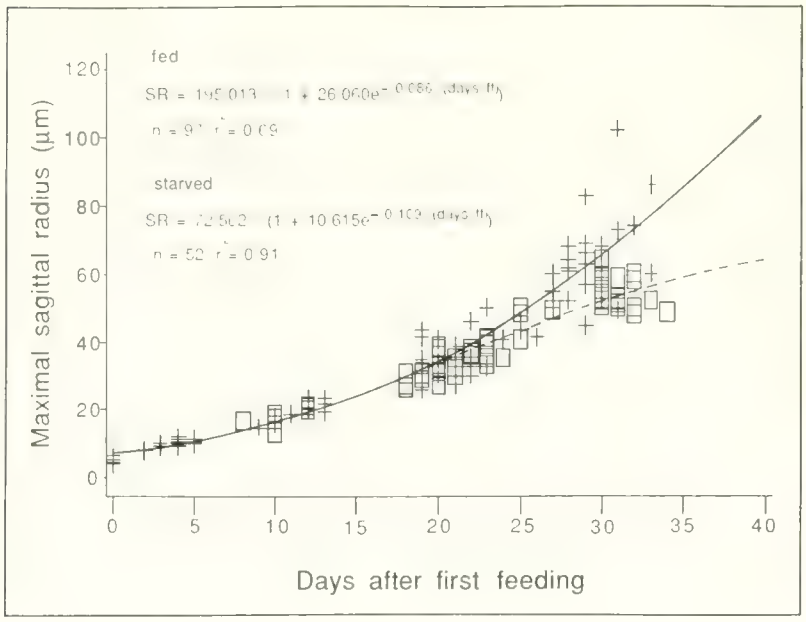

Figure 5
Nonlinear regression of sagittal radius (SR) on days after first feeding (days *ff*) of Atlantic menhaden larvae from control (solid line, +) and treatment (1–3 day starved, broken line, □) tanks. Model coefficients and other descriptive statistics are also given. Some symbols represent more than one observation.

significant ($p<0.0001$) and residuals were distributed at random over the entire size range examined, indicating a good fit of the logistic model to the log-transformed data. The relationship between sagittal radius and days after first feeding was also fit with a logistic function (Fig. 5). The regressions were highly significant (<0.001) and residuals were distributed at random, but the variance increased with age of the larvae. Predictions of sagittal radius from the regressions indicated that increment width increased from 0.6 μm at first feeding to 3.8 μm at 30 days in larvae from the control tanks, while increment width increased from 0.7 to1.6 μm in larvae from the treatment tanks.

Discussion

The results of our laboratory experiments indicate that microstructural growth patterns in sagittae of Atlantic menhaden can be used to accurately estimate age from first feeding, detect short-term variations in growth rate caused by starvation, and estimate the growth chronology of individual larvae. Age of individual larvae from first feeding can be estimated within ±3 days during the first month of life (based on inverse regression: Days after first feeding = a + b (increment count); Draper and Smith 1966, Rice 1987). Atlantic menhaden larvae appear to initiate increment formation at hatching, although growth increments formed prior to first feeding are narrow (<1 μm), poorly defined, and could not be consistently resolved with light microscopy. Poorly-defined increments observed during yolk feeding in the Atlantic menhaden have been observed during similiar periods in other species (Lough et al. 1982, McGurk 1984, Bolz and Lough 1983). The formation of these increments may be related to an immature circadian rhythm (Campana 1984b) and/or the presence of increments too narrow to detect using light microscopy (Campana et al. 1987). Formation of the first prominent growth increment in sagittae at first feeding may be related to the shift to exogenous feeding and related circadian activity patterns.

Transitions within the egg and larval stages of Atlantic menhaden were characterized by particular microstructural features. Hatching was characterized by a wide discontinuous zone, and the transition to exogenous feeding coincided with a prominent growth increment. Similiar patterns have been observed in other species (Brothers and McFarland 1981, Campana 1983, Lagardere and Chaumillon 1988). Particular microstructural features formed during the early life stages may be the result of changes in physiological metabolism, stress, and/or growth cycles that are generally associated with these transitions.

Studies that have examined the rate of increment formation in fish larvae reared under conditions promoting rapid growth have shown that growth increments form daily in most cases (Jones 1986). Atlantic menhaden larvae fed ad libitum formed increments at a rate of unity, consistent with the hypothesis that increments are formed daily in sagittae of well-nourished fish larvae. Estimates of statistical power obtained in our study indicate low variability about the relationship between increment count and days after first feeding and provide additional support that growth

increments are formed daily in sagittae of Atlantic menhaden larvae. A closely related species, the Gulf menhaden *B. patronus*, initiated increment deposition at first feeding and formed an average of one growth increment per day in sagittae (Warlen 1988). The frequency of increment formation in juvenile Atlantic menhaden held in enclosures also indicated that sagittal growth increments are formed daily (Simoneaux and Warlen 1987).

Starvation of larval Atlantic menhaden for 1–3 days did not result in the cessation of sagittal growth nor systematically alter the periodicity of increment formation from one increment per day. Larvae starved for 2- and 3-days formed increments at rates similiar to larvae which were fed continuously. Similiar results have been reported for other species reared under various feeding regimes, including starvation (Marshall and Parker 1982, Campana 1983, Eckmann and Rey 1987). However, other studies investigating formation of otoliths have found that periods of starvation may affect the rate of increment formation (Townsend and Graham 1981, Geffen 1982, McGurk 1984, 1987). Growth increments formed during starvation and periods of slow growth may be difficult to resolve due to their small size , generally <1 μm, which is near the limit of resolution of most light microscopes. This may have resulted in underestimation of the number of increments in two of the experimental groups of Atlantic menhaden larvae in our study and contributed to the apparent nondaily deposition rate. Theoretical daily increment width of larval Atlantic herring during early growth (first 2 weeks) was predicted to be below the limit of resolution of light microscopy (Campana et al. 1987). Examination of otoliths of fish exposed to suboptimal conditions indicated that age was underestimated using light microscopy compared with high resolution viewing by SEM (Jones and Brothers 1987, Bailey and Stehr 1988).

Microstructural growth patterns observed in sagittae of larval Atlantic menhaden support the hypothesis that variations in nutrition and environmental factors affecting fish growth are manifest as variations in increment width (Methot and Kramer 1979, Neilson and Geen 1982, 1985, Radtke 1987). The response of increment width to short intervals of starvation indicate that sagittae of Atlantic menhaden larvae may provide a reliable record of short-term (e.g., days) changes in feeding. The response time to starvation of Atlantic menhaden larvae examined in our study was rapid. Increment width of larvae starved for only 1 day declined significantly compared with fed larvae. The response time of increment width to cessation of starvation varied with the age of larvae. Mean increment width of larvae in the young age class increased to that of the controls within 3–4 days after starvation. Mean increment width of larvae in the older age class increased less rapidly after starvation than did that of the younger age class and did not reach that of controls during the recovery interval (4–6 days).

Our results indicate that microstructural growth increments in sagittae of Atlantic menhaden can be used to infer the dynamics of larval growth. In particular, examination of sagittal microstructure can be used to estimate the age of individual larvae from first feeding, detect stressful periods, and reconstruct the growth rate chronology of Atlantic menhaden larvae. We are currently investigating short-term (e.g., days) variations in growth rate of sea-caught Atlantic menhaden larvae, inferred from analysis of sagittal microstructure, in relation to meteorological and oceanographic variables (Checkley et al. 1988, Maillet 1988). Measurements of individual growth increments, although tedious to obtain, may allow inference about important events during the early life stages of fish. Variations in the width of growth increments from otoliths of fish larvae collected in nature could be analyzed for correlations with the timing of particular developmental and environmental events to determine their relative importance.

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Abstract.–The annual migratory cycle of Argentine hake *Merluccius hubbsi* was related to environmental conditions in the Southwestern Atlantic Ocean. In late summer–early fall, hake move northward and offshore towards feeding grounds. A southward and inshore migration towards spawning grounds occurs in early spring. The ends of the migratory circuit are associated with productive ocean fronts. Differences in the migratory pattern between 1978 and 1979 were tied to fluctuations in the latitude of the confluence of the Brazil and Malvinas currents along the shelf break.

Migratory Pattern of Argentine Hake *Merluccius hubbsi* and Oceanic Processes in the Southwestern Atlantic Ocean

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The Argentine hake *Merluccius hubbsi* is the most important species in Argentine fisheries: its landings make up approximately two thirds (in weight) of all Argentine fish catches. Fishery surveys carried out at different times of the year, together with data on the movements of the commercial fishing fleet, have revealed seasonal changes in hake distribution. The inshore spawning migration of adult hake on the Argentine shelf was first described by Hart (1946). Using data from a commercial trawler, Angelescu et al. (1958) showed the change in depth distribution of hake throughout the year. Christiansen and Cousseau (1971) and Bellisio et al. (1978) described the seasonal movements of the Argentine fishing fleet targeting on hake. An extensive research program sponsored by UNDP-FAO between 1968 and 1975 resulted in an improved knowledge of the distribution and migration of Argentine hake (FAO 1975). Otero and Kawai (1981) proposed the existence of two Argentine hake stocks, one migrating approximately between 35°S and 44°S and another moving between 44°S and 50°S. Chung and Tanaka (1985) investigated the displacements of hake using a 1-year series of research cruises. Otero (1986) used several years of commercial fishery data to describe the migration of hake, showing the progressive expansion of effort towards the southern part of the Argentine shelf.

Despite our knowledge of the seasonal distribution of hake, not much is understood about the oceanic conditions which contribute to define the migratory pattern of the species. The objective of this paper, therefore, is to explore the association between the migration of hake and environmental conditions in the southwestern Atlantic Ocean off Argentina and Uruguay. A usual approach is to treat fish distribution as a function of one or a few environmental variables (e.g., water temperature, salinity). Instead, emphasis is placed here on physical features, such as ocean fronts of diverse nature, which are an intrinsic part of the Argentine shelf ecosystem. I will discuss the relevance of these features to the different migratory stages (and, therefore, varying biological requirements) of hake. Historical fishery and hydrographic data are used to establish links between the distribution of hake and oceanic features; any such links may form the basis of specific hypotheses that can be rigorously investigated in the future.

Data and methods

The primary data used to determine the migratory pattern of hake include catch, effort (trawling hours), and area of operations (by 1-degree squares) reported by the Argentine offshore fishing fleet in 1978 and 1979. A detailed description of the fishery data is presented by Podestá

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(1987). Data from fishing surveys carried out between April 1978 and April 1979 by German and Japanese research vessels (Ciechomski et al. 1979a, Cousseau et al. 1979) are also incorporated in the discussion.

Monthly maps (not shown) of fishing effort and hake catch-per-unit-effort (CPUE) drawn from the commercial fishery data were used to track the migration of exploited concentrations of hake. The use of commercial fishing statistics to follow fish migration, however, has limitations. The fleet may be targeting on species other than the one being considered. Fleet movements, therefore, may be primarily associated with perceived fluctuations in the abundance of the target species. The Argentine offshore fleet targets mainly on hake; the proportion (in weight) of hake in the catches was >95% during most of the period studied. The proportion of shortfin squid (*Illex argentinus*) in the catches increased during May–July as a result of seasonal overlap in the distributions of both species. Even then, the Argentine fleet did not generally target on squid, which could be considered as bycatch (Juanicó 1982).

The use of fishery data to investigate migration relies on the fishermen's ability to locate the densest aggregations of hake. Several lines of evidence support this assumption. The hake fishery has been taking place for several years and the displacements of fish are well known. Monthly histograms of standardized hake CPUE show a moderately positive skewness (data not shown) that may be partly associated with a widespread knowledge of fish distribution (Quinn 1985). A comparison of alternative formulations for a monthly CPUE index, i.e., an average-of-ratios vs. a ratio-of-averages, confirms that effort was concentrated on areas of higher-than-average hake abundance (Otero 1986). This conclusion is also supported by spatial statistics of fishing effort and CPUE (Rothschild and Yong 1970).

To visualize better the patterns of hake movement, monthly latitudinal and longitudinal weighted averages of fishing effort and hake CPUE were computed according to the procedure described by Rothschild and Yong (1970). In some months, fishing effort was deployed in distinctly separate regions throughout the shelf. This may have reflected true operational differences in the fishing fleet as a consequence of separate centers of fish abundance. To take into account the discontinuity, I grouped all contiguous 1-degree areas, calculated the total fishing effort for each cluster of contiguous areas, and considered only major clusters (those in which effort was >5% of the effort in the most heavily exploited cluster). Most months showed only one valid cluster of areas and, at most, two clusters fulfilled the previous criteria. I computed the spatial statistics of effort for each valid cluster. For the CPUE statistics, the same clusters delimited above were used,

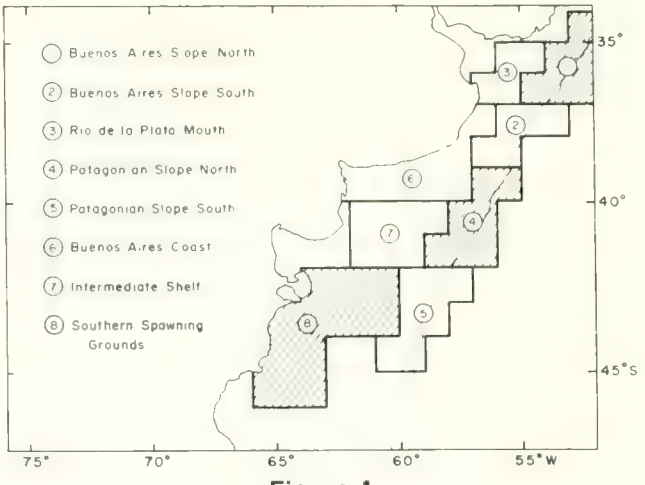

Figure 1

Geographic regions in southwestern Atlantic Ocean used for investigating interannual differences in hake migration. Stippled regions are discussed in the text.

but data were included only from areas where five or more trips had been reported, to reduce variability in CPUE values due to low levels of sampling.

As with most hakes (Jones 1974), tagging Argentine hake has proven so far to be impossible and, consequently, there are no estimates of migratory speed derived from tag returns of individual fish. As an approximation, I estimated hake migration speed by using the spatial statistics of fishing effort calculated above. I calculated the distances between the centers of effort in consecutive months, and then estimated daily migratory speeds by dividing the distances by 30 days (regardless of the specific months involved).

If the migratory pattern of hake is associated with environmental factors, year-to-year differences in their distribution may reflect fluctuations in oceanic conditions. I examined differences in the distributional pattern of hake between 1978 and 1979, and tried to relate those differences to environmental conditions.

A direct comparison of the commercial fishery effort and CPUE data is impossible because (a) there was a change in the format of the fishing tickets (the forms turned in by fishermen upon return to port) between 1978 and 1979, and (b) fishing effort had to be standardized separately for each year because of software limitations (see Podestá 1987).

A new fishing ticket was introduced in 1979 which, due to its design, increased uncertainty on the reported location of effort. To reduce the possibility of error, I grouped the data, originally reported for 1-degree squares, into eight larger geographical regions (Fig. 1).

Because fishing effort had been standardized separately for 1978 and 1979, the cumulative time density approach introduced by Mundy (1982) was used, which

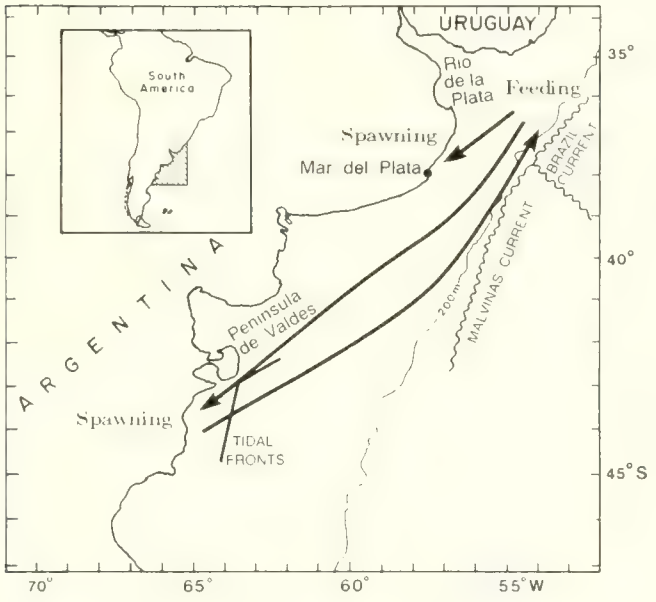

Figure 2

Schematic description of the annual migratory pattern of Argentine hake in southwestern Atlantic Ocean. Approximate locations of some oceanic features mentioned in the text are also shown.

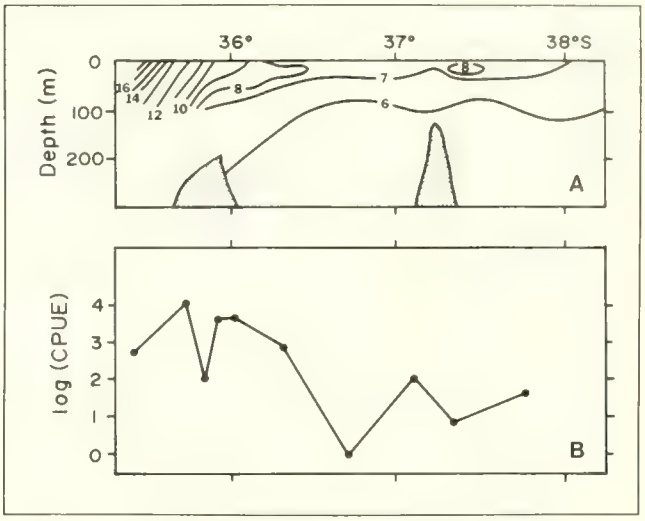

Figure 3

(*A*) Temperature section (°C) along the northern Argentine shelf break, July 1978. (*B*) Log of Argentine hake CPUE at fishing stations occupied at the same latitude as the hydrographic stations, but slightly shoreward. Date from the RV *Walther Herwig*.

does not require between-year consistency in the measure of effort. The technique is based on the fluctuations in fish abundance as a function of time in a fixed geographic reference frame and originally employed catch or CPUE data (Mundy 1982). However, the regions considered showed no fishing effort during some months and CPUE was undefined; the zero effort value, in contrast, was meaningful. Therefore, I used effort values (hours trawled per month) to construct the cumulative time density series in the manner described by Mundy (1982).

Results

Migratory pattern of hake

Figure 2 shows a schematic description of the migratory pattern of Argentine hake, derived from catch-and-effort statistics of the commercial fleet for 1978 and 1979 and complemented by literature reports. Hake show a cyclic northward-southward migration accompanied, respectively, by offshore-inshore movements.

The northernmost area reached by concentrations of hake exploited by the Argentine fleet is off Río de la Plata, between 34°S and 38°S. Hake arrive around May and stay through August, so this area can be considered the wintering grounds. During these months, hake concentrate along the outer shelf and continental slope.

Figure 3a shows a temperature section from hydrographic stations occupied along the shelf break, approximately between 35.5°S and 38°S, by the RV *Walther Herwig* in July 1978. The tightening of the isotherms in the northern part of the section (at about 36°S) indicates the confluence of the Malvinas Current, which flows northward carrying nutrient-rich subantarctic waters, and the subtropical waters of the southward-flowing Brazil Current (Olson et al. 1988). Figure 3b shows hake CPUEs in fishing stations occupied at the same latitudes as the hydrographic stations, but slightly shoreward. The highest densities of hake occurred near the Brazil-Malvinas confluence.

By the end of winter (September), a southward movement begins, accompanied by a corresponding inshore migration to shallower waters (Christiansen and Cousseau 1971, Bellisio et al. 1978). During the southward migration, fishing effort is widely scattered and CPUE values are relatively homogeneous throughout the shelf. This suggests a spatial dispersion of hake, which is not observed during the northward leg of the migration (Otero 1986).

The southward migration is associated with a movement towards spawning grounds. Mature female hake can be found year-round (Christiansen and Cousseau 1971), but most of the reproductive activity takes place in spring and summer (Ciechomski et al. 1979b). October and November are months of active spawning for at least some part of the stock(s). Commercial fishery statistics do not allow any conclusions on reproductive status, as only the weight of fish caught is reported.

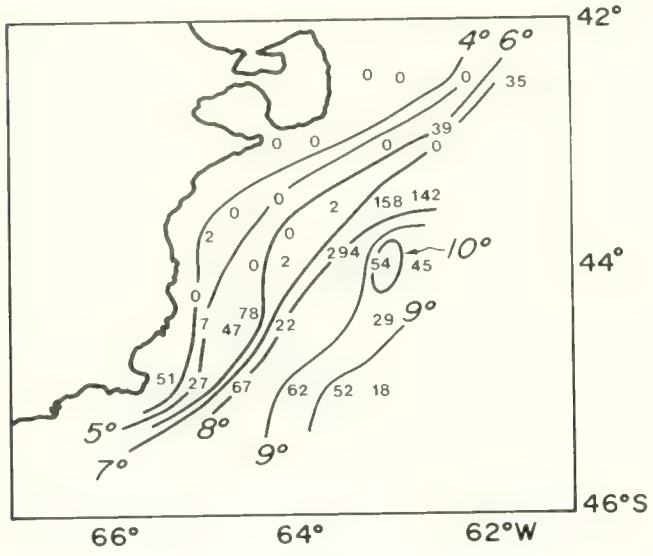

Figure 4

Argentine hake CPUEs (in hundreds of kg/hour) in the southern spawning area, south of Península de Valdés, Argentina, December 1978. Isolines correspond to surface-to-bottom temperature difference (°C), an indicator of water-column stratification; small values indicate well-mixed conditions.

I therefore examined data from egg and larval surveys carried out in early spring and summer of 1978 (Ciechomski et al. 1979b). Ciechomski and Sánchez (1983) established a well-defined relation between egg densities and corresponding adult concentrations.

In early spring (October through mid-November), there are two distinct centers of hake spawning: the northern catch between 36°S and 39°S and the southern between 42°S and 44°S, in waters <100 m deep (Ciechomski et al. 1979b). It is not clear what proportion of the fish spawn in each center, and whether fish that spawned in the northern center continue migrating south or, instead, move directly offshore.

Later in the season (December–January), several surveys showed that the area 42–47°S becomes the main spawning region. The largest concentrations of hake eggs and larvae in December 1978 were found in shallow waters at 44°S (Ciechomski et al. 1979b). Figure 4 displays the hake CPUEs obtained in the spawning area south of Península de Valdés, during cruise 9 (December 1978) of the *Shinkai Maru*.

In this area, features known as tidal fronts have been described by Carreto et al. (1986) and Glorioso (1987). The fronts separate stably-stratified waters offshore from well-mixed waters inshore. Vertical stratification is generated by surface heating; the well-mixed zone, on the other hand, results from stirring by strong tidal currents and winds (Carreto et al. 1986).

Water column stratification can be described by surface-to-bottom temperature differences, plotted on Figure 4. However, the transition from a well-mixed to a stratified regime and, thus, the location of the tidal front, are not apparent in this figure: temperature differences are >4°C, except in very shallow regions. This may have been due to the development of a shallow thermocline (~10 m) in inshore waters following a few days of calm weather. The location of the front is indicated instead by the transition from a shallow to a deeper (~35 m) thermocline (data not shown) which occurred in the vicinity of water column temperature differences of 7–8°C, as depicted in Figure 4. Highest hake CPUEs were observed near this transition; in contrast, hake CPUEs inshore of the front were very low.

The last portion of the migration, which closes the circuit, is the northward movement. This stage begins in February and lasts through May–June, when hake reach the wintering grounds. Fishing-effort maps suggest that the fish move north and across the shelf up to 40°S during February, and then continue northwards along the shelf break.

Spatial statistics

The spatial statistics are intended to represent "centers of mass" of the distributions of fishing effort or hake relative abundance during each month. Due to the uncertainty in effort location reports in 1979, the centers of fishing effort and hake CPUE are shown only for 1978 (Fig. 5).

The average positions of CPUE and effort showed cyclical north-south and east-west movements during a year. The monthly centers of CPUE and effort were quite similar, implying coincidence in the spatial distributions of fishing effort and apparent hake abundance. This suggests that the fleet was successful in locating dense aggregations of hake and lends confidence to the use of fishing-effort data to follow the commercial densities of migrating hake.

The multiple centers of effort in December, January, and February may be related to the existence of separate spawning groups of hake. On the other hand, the two centroids may merely reflect operational tactics of the fleet; although effort has been standardized to take into account differences in catching power, smaller vessels may lack the endurance or hold capacity required for a trip to the southern spawning grounds. Alternatively, fishermen may perceive that the catch rates in the northern and southern grounds are not so different as to make the longer trip worthwhile.

Speed of hake migration

Distances between monthly centers of effort and estimated speeds of migration are shown in Table 1. There was a bimodality in estimated displacement speeds throughout the year; the two modes corresponded,

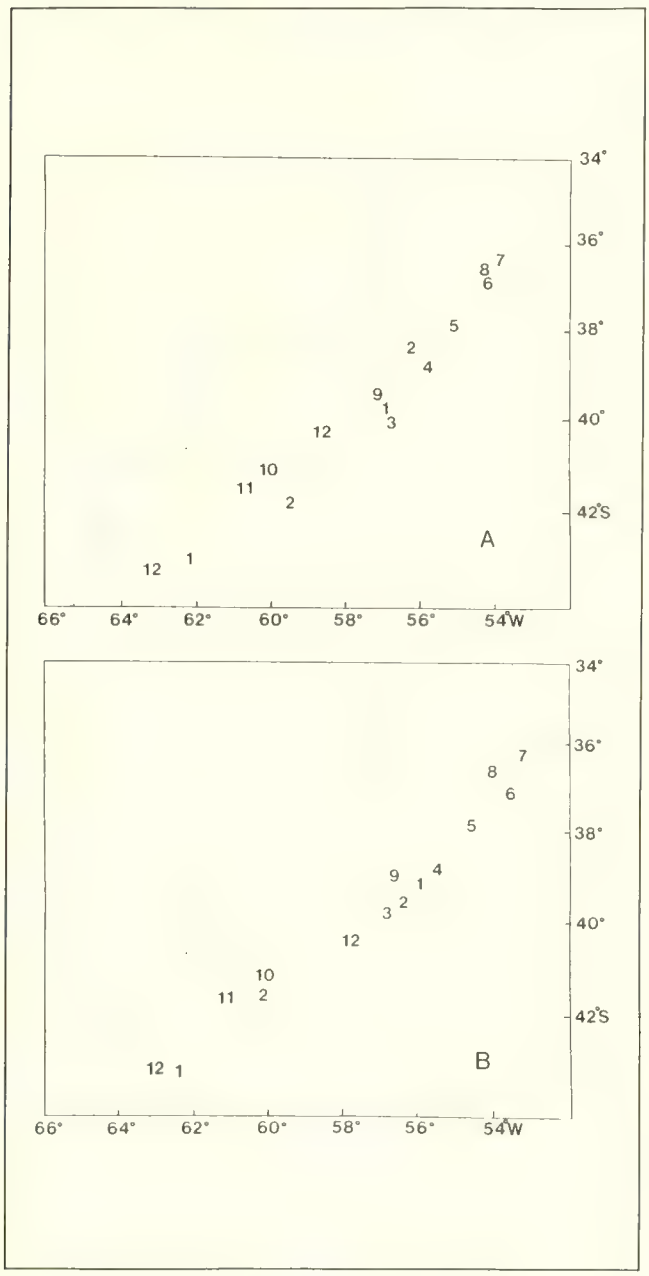

Figure 5

Monthly weighted latitude and longitude means of (a) fishing effort and (b) Argentine hake CPUE in southwestern Atlantic Ocean, computed from 1978 commercial fishery statistics. Numbers indicate months.

Table 1

Distance between consecutive monthly centers of fishing effort in southwestern Atlantic Ocean during 1978 and Argentine hake swimming speeds required to cover those distances in 30 days. When two centers existed in a month, they were indicated as northern (N) and southern (S). Segments marked with an asterisk are considered to be inconsistent with the migratory pattern of hake.

Segment	Distance (km)	Speed required	
		m/sec	km/day
Jan(N)–Feb(N)	128	0.05	4.3
(*) Jan(N)–Feb(S)	297	0.11	9.9
(*) Jan(S)–Feb(N)	636	0.25	21.2
Jan(S)–Feb(S)	244	0.09	8.1
Feb(N)–Mar	144	0.06	4.8
Feb(S)–Mar	276	0.11	9.2
Mar–Apr	131	0.05	4.4
Apr–May	99	0.04	3.3
May–June	122	0.05	4.1
June–July	48	0.02	1.6
July–Aug	37	0.01	1.2
Aug–Sep	351	0.13	11.7
Sep–Oct	285	0.11	9.5
Oct–Nov	49	0.02	1.6
Nov–Dec(N)	188	0.07	6.3
Nov–Dec(S)	264	0.10	8.8

respectively, to speeds of 6–11 km/day and 1–4 km/day (Table 1). Higher speeds, obviously, are associated with periods of active migration.

The estimated speeds of the northward and southward (i.e., feeding and spawning) migrations were similar. Estimated speeds during the most active periods of southward displacement were 11.7 km/day (August–September) and 9.5 km/day (September–October). The latter value was only slightly higher than that computed for the active northward migration, 9.2 km/day (February–March). If a significant difference in southward vs. northward migrating speed exists, it probably cannot be detected using coarse fishery statistics.

The migration speeds estimated above must be considered only as a first approximation, but they generally agree with values reported for a similar species. Francis (1983) estimated swimming speeds for Pacific hake *Merluccius productus* of different ages based on timing of sequential appearance at different latitudes. His estimated speeds for the age classes 4–7, those predominant in Argentine hake catches, range from 9 to 12 km/day. Ermakov (1974; cited in Bailey et al. 1982) concluded from direct observation of a school that the northward migration of Pacific hake is at speeds of 5–11 km/day.

Interannual variability in the migratory pattern of hake

Cumulative time density of fishing effort is shown in Figure 6 for three regions: Buenos Aires slope north (region 1), Patagonian slope north (region 4), and southern spawning grounds (region 8). The values shown in the figures for each month represent the proportion of yearly regional effort accumulated up to the end of

that month. Monthly values are joined by line segments in the figures: segments with steep slopes are associated with a relatively large proportion of total regional effort. Conversely, if little or no effort took place within a month, the corresponding segment will be nearly horizontal.

The interpretation of the cumulative time density curves is related to the pattern of hake migration. For example, effort started to accumulate in region 1 (Fig. 6a) around April or May, when fish first arrived in this area on the northward leg of their migration. The S-shaped 1978 curve indicated that there was a single peak in the deployment of effort during winter months (May–August). In contrast, in 1979 most of the effort was deployed between March and June, with a secondary peak in September–October.

In region 4 (Fig. 6b), effort accumulated rapidly during February, March, and April of 1978, as the hake were migrating northwards along the shelf break. Afterwards, effort decreased greatly. In 1979, the initial effort was much like the previous year's, but it tapered off until June, July, and, particularly, August (winter). Effort in winter months was not observed in 1978.

In region 8 (Fig. 6c), the effort patterns were remarkably similar for both years. The curves were flat between March and September, as both the fish and the fleet were absent from the region. During October, November, and December the spawners arrived in the area and fishing effort accumulated rapidly.

Interannual differences between cumulative time density patterns were statistically analyzed using the Kolmogorov-Smirnov (K-S) two-sample test. Because of the large N values (the annual total number of hours trawled in a region), all the K-S tests were significant (see Rugolo 1984), including those for regions not shown. As a consequence, the discussion will focus on regions 1 and 4, where the patterns appeared to differ most between the two years.

From the patterns in regions 1 and 4, it appears that the fishing fleet (and, thus, hake) was located further south in 1979 than in 1978. The spatial statistics of fishing effort also reflect a more southerly deployment of effort in 1979. The latitudinal means of fishing effort for July and August 1978 were, respectively, 36.4°S and 36.6°S; the corresponding values for 1979 were 38.2°S and 40.2°S. That is, the "center of mass" of fishing effort in the winter of 1979 was located 2–4 degrees of latitude further south along the shelf break than in 1978. The changes in hake distribution may reflect interannual differences in environmental conditions.

The northernmost extension of the hake feeding migration, reached during June–August, is associated with the Brazil-Malvinas confluence. The confluence is

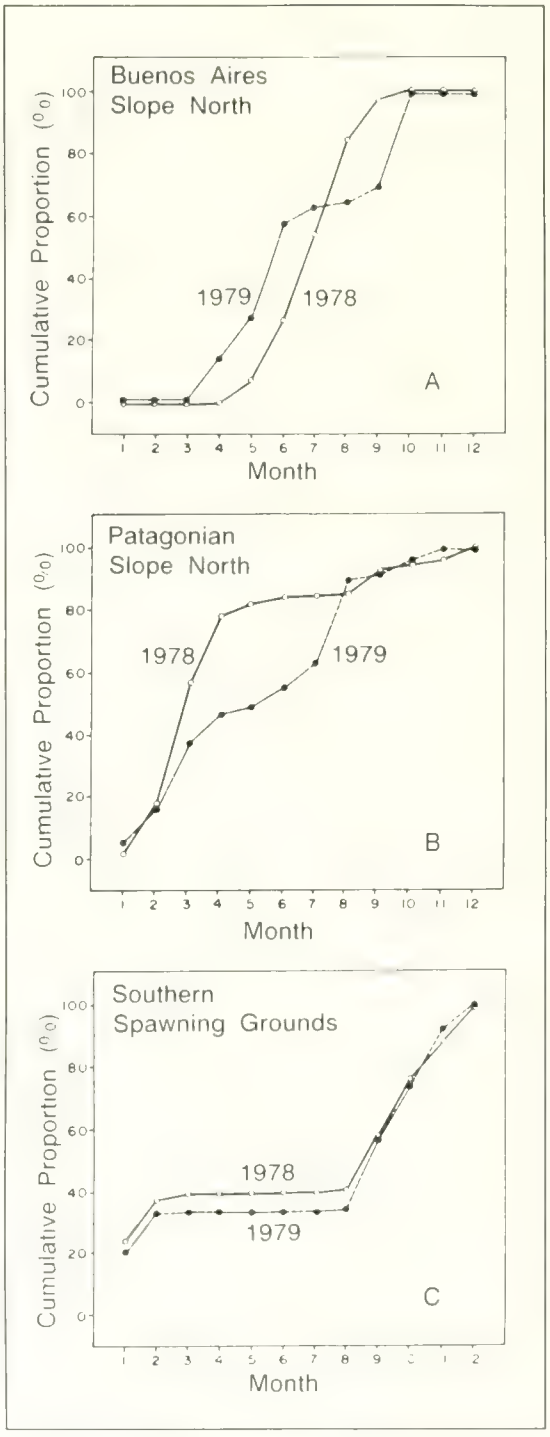

Figure 6

Cumulative time densities for (A) Buenos Aires slope north (region 1), (B) Patagonian slope north (region 4) and (C) southern spawning grounds (region 8). Location of regions is shown in Figure 1.

an effective barrier for adult hake of commercial size: aggregations of hake found north of it are mainly formed by juveniles (Rojo and Silvosa 1969). Olson et al. (1988) showed considerable fluctuations in the

latitude of the Brazil-Malvinas confluence along the shelf break. Shifts in the position of the confluence plausibly could have been responsible for the differences in hake distribution between 1978 and 1979.

Hydrographic stations occupied by the RV *Walther Herwig* during July 1978 placed the Brazil-Malvinas confluence along the shelf break at about 36°S. In August 1978, the confluence must have been located north of 37°S, as temperatures characteristic of Brazil Current waters were not observed during a cruise carried out by the RV *Shinkai Maru* that reached approximately that latitude (data not shown).

No hydrographic data were available to locate the confluence in July–August 1979. Instead, I used weekly GOSSTCOMP (global ocean sea surface temperature computation) charts for the period 3 July– 28 August 1979. The charts were produced from satellite data by the U.S. National Oceanic and Atmospheric Administration (Brower et al. 1976). The 10°C and 12°C surface isotherms were considered to represent the Brazil–Malvinas confluence at this time of the year. The approximate latitudes at which those isotherms occurred along the shelf break are displayed in Figure 7.

In early July 1979, the confluence was located at about 37°S, only slightly further south than in July 1978. During the last 2 weeks of July 1979, however, it moved to the south, reaching about 42°S by the end of the month. During August 1979, the confluence was generally located around 40°S. The deployment of fishing effort during July–August 1979 coincided roughly with the confluence locations deduced from the GOSSTCOMP charts. This seems to support the hypothesis linking shifts in the position of the Brazil-Malvinas confluence and hake distribution in 1978 and 1979.

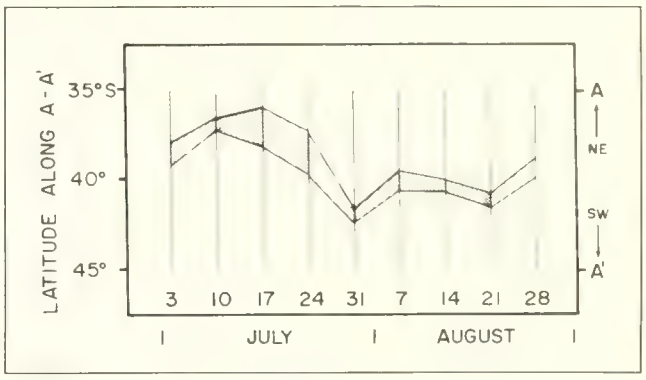

Figure 7

Approximate latitude of the Brazil and Malvinas currents confluence along the shelf break, July–August 1979, derived from GOSTCOMP charts. Each vertical line corresponds to a weekly sea-surface temperature chart. Shaded area represents projection of the 10- and 12°C isotherms along the shelf break, assumed to represent the position of the confluence.

Discussion

Feeding migration

The need to find an adequate food supply for maintenance, growth, and reproduction may have contributed to shape the migratory pattern of Argentine hake. Adult hake feed actively after spawning (Hart 1946). The postspawning offshore migration of adults towards the shelf break, then, may correspond to a search for abundant food sources.

The western edge of the Malvinas Current, from about 40°S to its confluence with the Brazil Current, plays an important role in the northward migration of hake, as the fish are closely associated with it for 5–6 months of the year. The boundary between shelf and Malvinas Current waters can be characterized as a shelfbreak front. Shelfbreak fronts elsewhere have been associated with high biological productivity and fishing intensity (Fournier et al. 1979).

The high productivity of the Malvinas front has been described from ship data (Hubold 1980a,b and references therein). More recently, remote sensing techniques have confirmed this feature: images collected by the Coastal Zone Color Scanner (CZCS) were used to monitor nearsurface concentrations of phytoplankton pigments and, indirectly, phytoplankton biomass. High phytoplankton concentrations occurred along the shelfbreak through spring and summer; in contrast, phytoplankton biomass across most of the shelf decreased rapidly following the late September–early October spring bloom. The shelfbreak, therefore, possibly represents one of the few places where forage is abundant during the summer, following the hake's spawning.

After a second bloom ends on the shelf in the fall (late March–early April), phytoplankton biomass along the shelfbreak remains high into late April. This may in turn support elevated zooplankton concentrations in subsequent winter months (Hubold 1980b), although at that time phytoplankton biomass is low.

The large phytoplankton biomass along the shelf break is probably the result of enhanced supply of nutrient-rich Malvinas Current waters into the euphotic zone, which could happen through a variety of processes. Small-scale eddies along the edge of the Malvinas Current may upwell nutrient-rich waters. This has been shown to occur along the edge of the Gulf Stream, resulting in an increase in phytoplankton and zooplankton biomasses (Paffenhöffer et al. 1984). Dickson et al. (1980) suggested that the interaction between coastally trapped waves propagating along the slope and bottom topography at the shelfbreak could enhance upwelling. The generation of internal tides at the shelfbreak, coupled with episodic wind stress, may

increase vertical mixing, again injecting nutrients into the upper layers (Mazé et al. 1986). Additionally, the tilt of the isopycnals or the interleaving of water masses at the front would enhance vertical stability, retaining phytoplankton cells in the euphotic zone (Fournier et al. 1979).

The increased phytoplankton biomass along the shelf break supports large concentrations of zooplankton (Hubold 1980a); species on which pelagic fish feed (e.g., calanoid copepods) are very abundant (Carreto et al. 1981a, b). Species from higher trophic levels also aggregate at the front.

The distribution pattern of anchoita *Engraulis anchoita*, an extremely important prey for hake, is closely associated with the shelfbreak front (Brandhorst et al. 1971). While hake and anchoita coincidentally migrate offshore and then northward along the slope in autumn, the former actively feed on the latter (Ciechomski and Sánchez 1983).

During the northward migration, other components may appear in the hake's diet, such as myctophids associated with the Malvinas Current (e.g., *Gymnoscopelus* spp., *Lampanyctus* spp., and *Myctophum* spp.) and shortfin squid *Illex argentinus* (Cordo 1981). Dense concentrations of shortfin squid occur along the shelfbreak in late fall (Otero et al. 1981). Squid is increasingly found in the stomachs of medium and large hakes between April and July (Angelescu and Cousseau 1969, Cordo 1981). Given their high food assimilation efficiency (Caddy 1983), squid probably play an important ecological role in rapidly transferring energy from lower trophic levels to hake.

When hake reach the northernmost end of their feeding migration in winter, they have access to a large abundance of prey from a variety of closely located environments. In addition to the species found along the shelfbreak, they may feed on anchoita wintering in midshelf waters or on subtropical myctophids from Brazil Current waters. Further south or inshore, in contrast, pelagic fish become rare and the overall abundance of prey decreases rapidly (Angelescu and Cousseau 1969).

Spawning migration

The present migratory pattern of hake may have evolved to maximize chances of reproductive, as well as feeding, success. Starvation is a major source of larval mortality for most fish species. The choice of spawning sites with adequate concentrations and size ranges of larval food may have a great influence on survival. Hake larvae feed almost exclusively on zooplankton, particularly small calanoid copepods (Ciechomski and Weiss 1974).

Regional shifts in hake spawning activity may be related to the seasonal pattern of productivity along the shelf. The phytoplankton spring bloom begins in the north and progresses southward (Carreto et al. 1981a). The spawning activity between 36°S and 38°S in early spring, then, may be tied to increased zooplankton availability resulting from the bloom. However, satellite imagery shows that postbloom phytoplankton biomass here remains low throughout late spring and summer and apparently does not support an extended spawning season. Later in the season, the bulk of the spawning activity takes place between 42°S and 44°S, where production possibly may continue during the summer because of the presence of tidal fronts.

The tidal fronts appear to be associated with enhanced phytoplankton biomass: Carreto et al. (1981a) observed integrated chlorophyll concentrations >200 mg/m^2 at the beginning of October. The increased biomass may be due to enhanced nutrient supply by horizontal mixing from the mixed side or by vertical mixing through the pycnocline. Carreto et al. (1986) found high surface concentrations of nitrates (>6 μm) on the mixed side.

The existence of the tidal fronts has only recently been noticed and, consequently, there is relatively little information on their biological productivity. Nevertheless, high concentrations of zooplankton (expressed in dry weight) have been reported along the fronts (Angelescu and Prenski 1987). There is additional indirect evidence for the relatively high productivity of these features: hake larvae in this area are found to be in an excellent nutritional state, better than elsewhere on the shelf (R. Sánchez, INIDEP, C.C. 175, Playa Grande, Mar del Plata, Argentina, pers. commun., Feb. 1989). Additionally, adult hake find abundant anchoita and squid in the vicinity of the fronts (Angelescu and Prenski 1987).

The tidal fronts occur throughout the summer, for as long as the offshore side of the front remains stratified. Satellite imagery shows that this area, together with the shelfbreak, are the only places where near-surface phytoplankton biomass remains high throughout the summer. The integrated spring–summer production of the tidal fronts area, therefore, may possibly be higher than in most parts of the shelf, although this requires confirmation.

Another factor relevant to the selection of a spawning site is the subsequent transport of eggs and larvae to (or, alternatively, their retention within) areas suitable for further development. Argentine hake show a wide temporal and spatial spawning range: hake eggs are found on the shelf practically year-round. Nevertheless, the gonads do not mature more than once during the main spawning period of spring–summer (Christiansen and Cousseau 1971), suggesting that a number of groups of spawners release eggs throughout a large area and an extended time interval. Argentine hake

exhibit a ubiquitous spawning strategy throughout the shelf and, therefore, do not appear to be dependent on larval drift and retention conditions. A possible exception is the shelfbreak area: despite its importance in supporting abundant forage supplies, this area is not a suitable spawning location. Eggs and larvae spawned along the shelfbreak would most likely be carried offshore.

The circulation pattern of the Argentine shelf, as it contributes to larval drift or retention, has not been described in adequate detail. Circulation gyres or topographical features that may contribute to the separation of hake spawning groups on the Argentine shelf are not apparent. If different spawning groups exist, the specificity of their place and time of spawning or, equivalently, the degree of mixing among them, remains unclear.

This work identified apparent differences in the migratory pattern of hake between 1978 and 1979, which were tied to the location of the confluence of the Brazil and Malvinas currents along the shelfbreak. Sosa et al. (1976) mention 60–100 mile changes in Argentine hake distribution associated with wind-induced short-term fluctuations in the position of the confluence. Repeated monitoring of the confluence location through satellite imagery (cf. Olson et al. 1988) would make it possible to further investigate this association.

In summary, the cyclic migration of commercial densities of Argentine hake was roughly described using data from commercial fishing operations. The migratory pattern has evolved to maximize the chances of successful spawning, while ensuring an adequate food supply. During their migratory cycle, hake take advantage of productive ocean features.

A number of issues remain unclear, such as the existence of different spawning groups and the degree of mixing among them. There is little information on the recruitment variability in Argentine hake, so one cannot speculate on the relationship between migratory pattern and recruitment success. The circulation on the Argentine shelf and its influence on larval drift or retention requires much study. Finally, the continued availability of prey for hake larvae throughout the summer in the tidal-fronts environment (which would lead to the bulk of spawning taking place there) needs to be confirmed.

Acknowledgments

Comments by F. Williams, N. Ehrhardt, D. Olson, J. Powers, and three anonymous reviewers are appreciated. Support was provided by the Office of Naval Research and by a National Research Council Research Associateship at NASA's Goddard Space Flight Center. Data from the Argentine fishing fleet were supplied by Subsecretaría de Pesca, Buenos Aires, Argentina. The *Shinkai Maru* and *Walther Herwig* data were provided by Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina. Travel to compile the data was funded by the Tinker Center of the University of Miami.

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Abstract.—Knowledge of population dynamics and production of dominant benthic organisms on the northwestern Atlantic continental shelf is important for developing or interpreting models addressing ecological or fishery management questions. This paper estimates the recruitment frequency and success, life span, growth rate, and production of a major component of the sand-bottom benthic community in this region: the common sand dollar *Echinarachnius parma* (Echinodermata: Echinoidea). These estimates are based on size-frequency data collected at least annually between 1977 and 1985 from three sites in the Middle Atlantic Bight and one site on Georges Bank. Larval recruitment of *E. parma* to the sites was mostly annual, but persistent cohorts were irregular. Average life span was about 8 years with some rare, larger, and presumably older animals present; the maximum size found was 54 mm. A time series of modal size progressions suggests mean growth in body width ranged from 3.5 to 6 mm/yr over a period of at least 5 years, with growth curves for cohorts appearing to be sigmoidal. Annual production: biomass ratios for definable cohorts varied with age, ranging from −0.04 for senescent older cohorts to 8.10 for juveniles.

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Population Dynamics, Growth, and Production Estimates for the Sand Dollar *Echinarachnius parma*

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Information on growth and production rates of major marine taxa can support the development of better ecological and fishery production theories or models (Winberg 1971, Greze 1978). Echinoderms are one of the major marine benthic taxa; however, information on their growth and production rates is scarce. For example, production estimates are currently available for little more than a dozen species worldwide (Richards and Riley 1967, Zaika 1972, Miller and Mann 1973, Buchanan and Warwick 1974, Greze 1978, Warwick et al. 1978, Warwick and George 1980).

On the Atlantic continental shelf north of Cape Hatteras, North Carolina, the sand dollar *Echinarachnius parma* is an abundant echinoderm of fine to medium-sand habitats (Coe 1972, Wigley and Theroux 1981). Because of its relatively large size (>50 mm) and population densities which can reach hundreds of adult individuals per m^2 (Caracciolo and Steimle 1983), it may be a "keystone" species as defined by Paine (1969), i.e., a major factor in structuring the benthic community by dominating habitat and detrital food use. Stanley and James (1971) conclude this species to be the second most important factor, after major storms, in reworking surface sediments. This sediment reworking can disturb smaller epifaunal benthic species and larval recruitment, which can include shellfish species of commercial interest. For example, Richardson et al. (1983) studied an *E. parma* community off Rhode Island, and studies of similar Pacific and Atlantic sand dollar species *Dendraster excentricus* and *Mellita quinquiesperforata* by Smith (1981), Creed and Coull (1984), and J.A. Reidenauer (Dep. Oceanogr., Fla. State Univ., Tallahassee, FL 32306, pers. comm., July 1985) found that aggregations of sand dollars substantially alter benthic macrofauna community structure, especially for tube dwellers and meiofauna.

Besides its potential role in controlling benthic community structure, *E. parma* also occurs frequently in the diets of some commercially/recreationally valuable fish, including haddock *Melanogrammus aeglefinus*, summer flounder *Paralichthys dentatus*, American plaice *Hippoglossoides platessoides*, scup *Stenotomus chrysops*, tautog *Tautoga onitis*, and yellowtail flounder *Limanda ferruginea* (Bigelow and Schroeder 1953, Coe 1972, Maurer and Bowman 1975, Collie 1987). However, its food value (Kcal/g) is half that of other common benthic prey, e.g., polychaetes or crustaceans (Steimle and Terranova 1985). Despite wide use of *E. parma* as prey, extensive populations of this echinoderm, primarily of individuals too large to be eaten by most predators, may be an energy sink (Mercer 1982). For example, *E. parma* can comprise 40-50% of the total benthic macrofaunal biomass on Georges Bank (Steimle 1987).

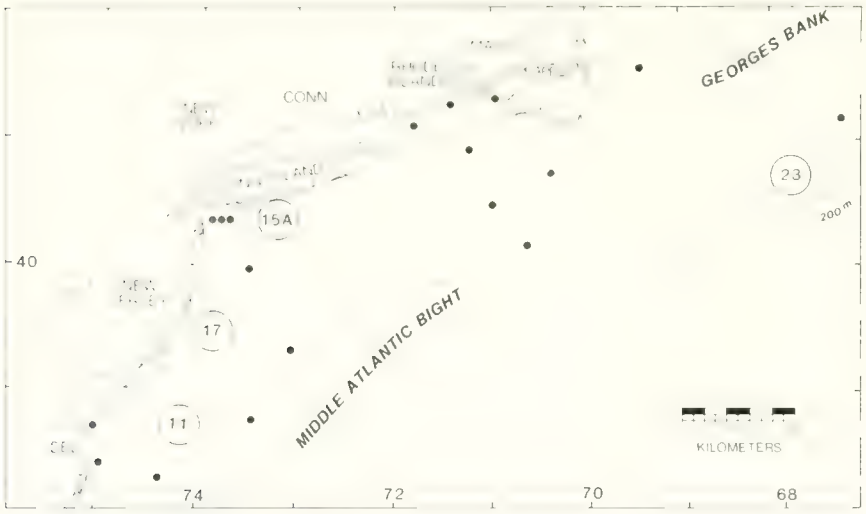

Figure 1
Station locations of the four study sites in the Middle Atlantic Bight–Georges Bank area. Other sites examined which did not produce reliable samples of *Echinarachnius parma* are also included (●).

Several studies have examined aspects of *E. parma*'s life history (for review, see Caracciolo and Steimle 1983). Only two studies have examined its growth (Cocanour 1969, Graef 1977) and none its production. Since *E. parma* can be a major contributor to the overall benthic community biomass, estimates of its production could greatly support an estimate of total community production. Warwick (1980) has shown that a major proportion of total community production is often attributed to one or a few species.

The purpose of this study was to examine *E. parma* size frequencies from a series of at least annual collections to provide information on the species' population structure, dynamics, and growth, and to estimate its production at stations in the Middle Atlantic Bight and on Georges Bank. The term "production" is used in this paper to indicate the amount of biomass added to a unit of bottom area per year.

Material and methods

Echinarachnius parma were obtained from archived benthic collections made at three stations (11, 15A, 17) in the Middle Atlantic Bight and one station (23) on southwestern Georges Bank (Fig. 1). Water depths at these stations were 20 m (Stn. 17), 30 m (Stn. 15A), 50 m (Stn. 11), and 70 m (Stn. 23).

The archived collections consisted of 3–5 replicate 0.1-m^2 Smith-McIntyre grab collections at each station sampled on a quarterly to annual basis, 1978 to 1985, as part of the Northeast Monitoring Program (NEMP). Collection periods varied slightly between stations (see Figures 2–5 for specifics). Grabs were handled to minimize loss of sample by surficial material washout; grabs suspected of being excessively disturbed were resampled. The samples were washed through 1.0-mm mesh sieves prior to 1980, and through 0.5-mm mesh sieves thereafter. While *E. parma* larvae are reported to undergo metamorphosis and settle to the seabed from the plankton at a width of about 0.4 mm (Cocanour 1969), the 1.0-mm sieve collected most postlarvae because few were collected on the 0.5-mm sieve when both sieve sizes were used together in 1980 and 1981. The sieved benthic samples were fixed in 10% buffered formalin, transferred to 70% ethanol within a few days, and later sorted.

Size-frequency distributions were based on measuring the diameter of each individual, parallel to the anal pore margin of the test, using either an ocular micrometer or vernier caliper. To estimate the ash-free dry weight (AFDW) of different cohort size classes, additional *E. parma* specimens were collected at the above sites and frozen, then sorted into 5-mm size groups covering the 5–50 mm size range, with each group containing 3–10 individuals, as available. Each size group was dried for 12 hours at 60°C and ashed for 4 hours at 500°C to produce a mean AFDW value per mean width (L in mm) and the regression; $AFDW = 0.02L^{2.55}$ ($r^2 = 0.991$). Overlapping cohorts were initially separated by probit graphical analysis (Cassie 1954), and these estimates were refined by the NORMSEP program (Tomlinson 1971) to separate overlapping distributions. Growth rates were estimated by modal progression analysis of the time series of size-frequency histograms (Figs. 2–5) for collections at each station. Production estimates are based on Crisp's (1971) growth-increment survivorship-curve method for populations with distinguishable recruitment and age classes (cohorts). Recruitment events in the Middle Atlantic Bight were assumed to be the result of fall–winter spawning, based on when recruits are first detected in

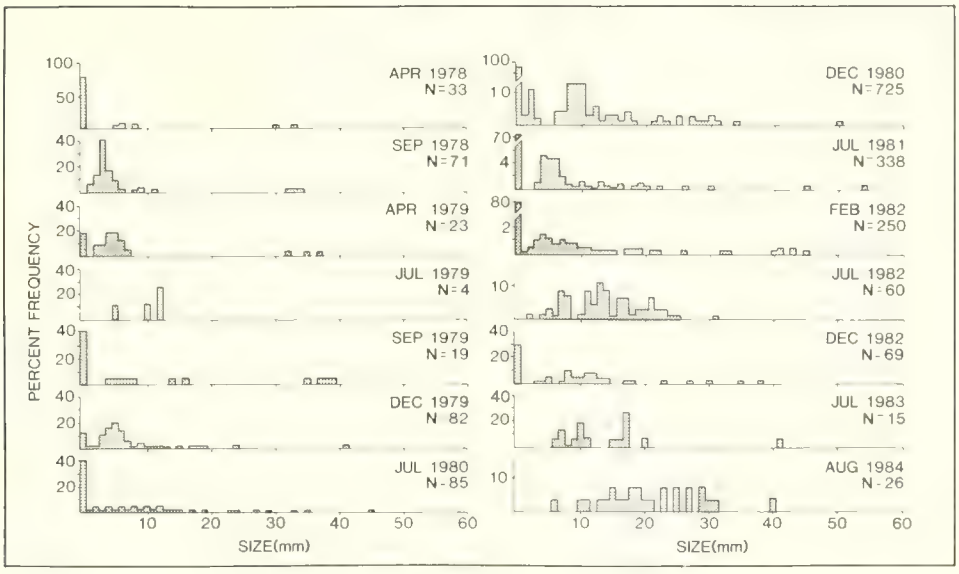

Figure 2
Echinarachnius parma size-frequency histograms per collection at station 11, Middle Atlantic Bight.

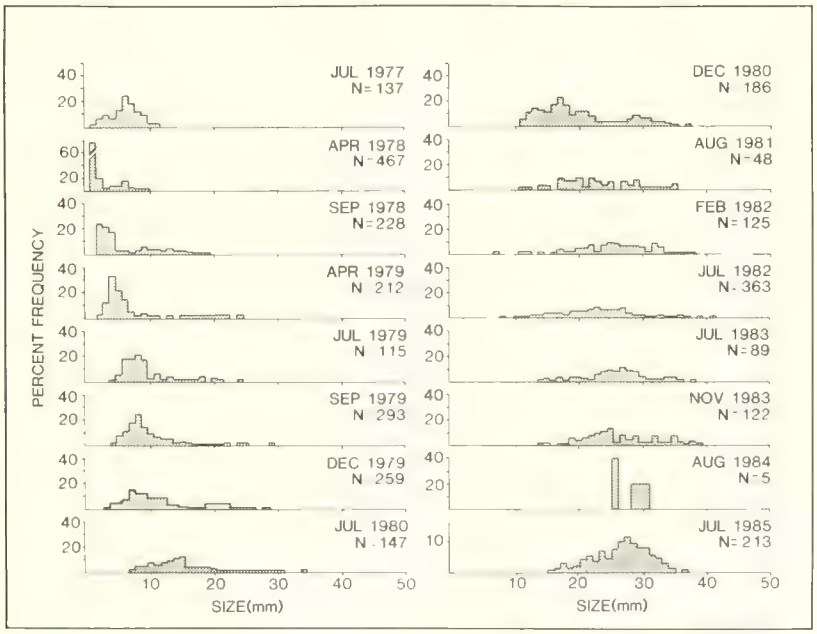

Figure 3
Echinarachnius parma size-frequency histograms per collection at station 17, Middle Atlantic Bight.

the samples (winter–spring) and thus identified by the pair of years covering the probable peak spawning period. The recruitment season was estimated, in some cases, from back-calculations based on growth curves. Ages assigned to each cohort are based on inspecting the length-frequency histograms and noting when recruitment, i.e., >2 mm size mode, was apparent. These can be considered relative ages, although it is highly probable they represent absolute age (±3 months) if it is assumed that a delayed metamorphosis of the larvae is not normally a major problem; there is no evidence to suggest otherwise.

The reliance on size-frequency analysis for growth and production estimates assumes (1) frequency modes represent cohorts, a reasonable assumption when recruitment period can be determined and modal shifts can be traced over a period of time, and (2) that the size distribution within each cohort was normal or representative of the true population and unbiased. A departure from normality may not be critical to the accuracy of mean size estimates (McNew and Summerfelt 1978). The sample sizes were often below the minimum (400) suggested by Cohen (1966) to separate accurately two cohorts in a single size-frequency analysis, with a larger sample needed for separating more than two

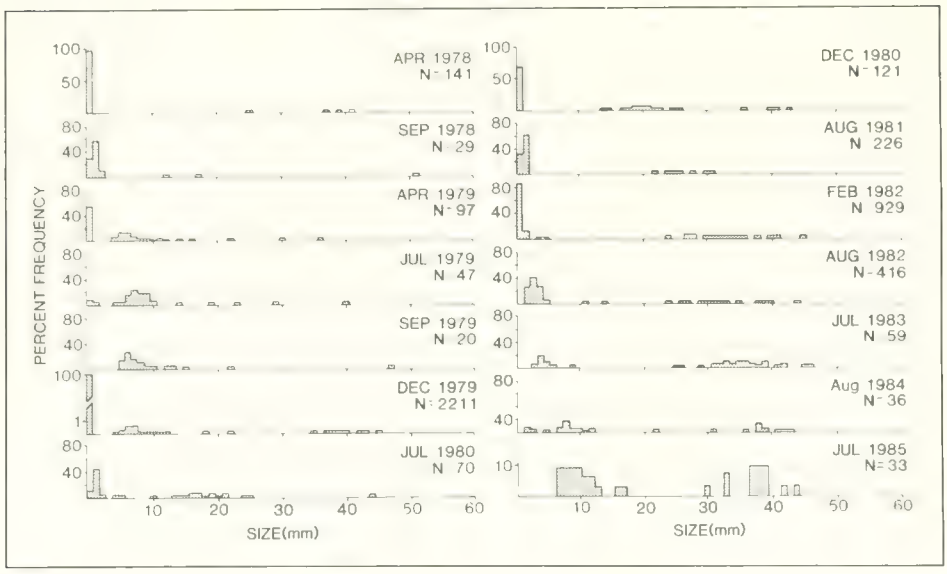

Figure 4

Echinarachnius parma size frequency histograms per collection at station 15A, Middle Atlantic Bight.

groups. The time series of population size-frequencies available in this study could estimate poorly defined cohorts and modal peaks by visual examination of the overall modal patterns in the time series.

Results

The size-frequency distributions, grouped into 2-mm size classes for all collections at each station, show a high degree of variability in population structure (Figs. 2–5). The distributions for Station 11, off Delaware Bay (Fig. 2), show a population with a variety of size classes evident in all collections; cohort definition is often weak, largely because of small sample sizes for most collections. Size-frequency distributions at Station 17, off Central New Jersey (Fig. 3), in contrast to Station 11, show a very limited population, restricted entirely to two annual recruitments in 1976 and 1978. Both of the two cohorts at Station 17 appear to persist until at least 1985 (the last collection of the study), although they were inseparable after 1981. There is no evidence of any additional recruits, even though the population reached a size, >27 mm, when spawning should occur (Ruddell 1977). The situation at Station 15A, off Fire Island, is similar to that of Station 11, with several sizes present in the population subsequent to initial collections (Fig. 4). There appear to be two recent strong cohorts, that of 1978 and 1982. Some non-persistent recruitment was evident in other years, however. The *E. parma* population structure at station 23, on northeast Georges Bank, was similar to that of Station 17, with no evidence of a population prior to 1978 and with the 1978 and 1979 cohorts the strongest, although non-persistent recruitment was noted for other years sampled.

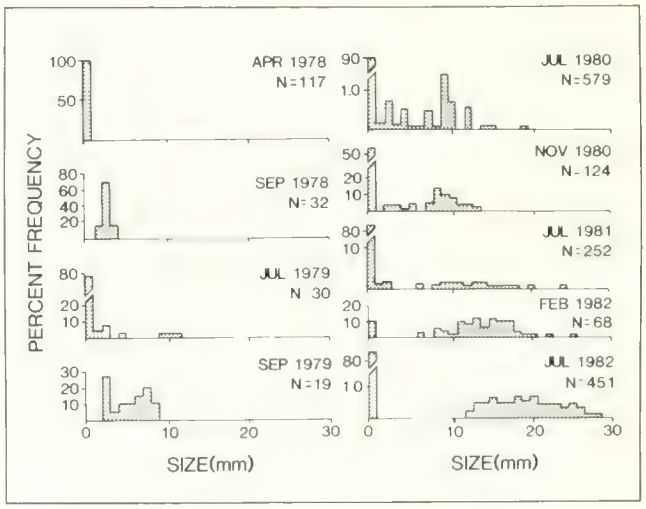

Figure 5

Echinarachnius parma size-frequency histograms per collection at station 23, southwestern Georges Bank.

The estimated growth curves (based on change in cohort's modal size progressions over time) of persistent and prominent cohorts at Stations 15A, 17 and 23, were sigmoidal (Figs. 6–8). The highly variable size-frequency distributions at Station 11 (Fig. 2) did not produce reliable modal trends to use for growth estimates. The mean cohort growth rates, approximated from modal progression analysis for definable cohorts ranged from 4.0 to 6.5 mm per year (Table 1).

Table 2 summarizes the estimated annual production (P), mean biomass (B), and P:B ratio for each cohort, and the total annual population production and P:B ratio for each station, showing much variability. A comparison of individual-cohort annual P:B ratios with

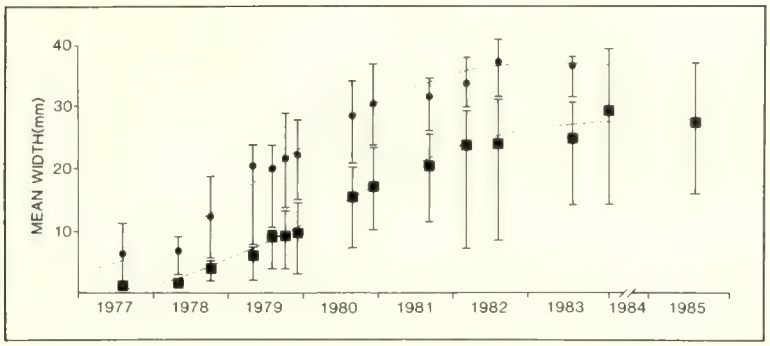

Figure 6
Growth curves from the shift of the mean widths of prominent *Echinarachnius parma* cohorts, over time, at station 17, Middle Atlantic Bight.

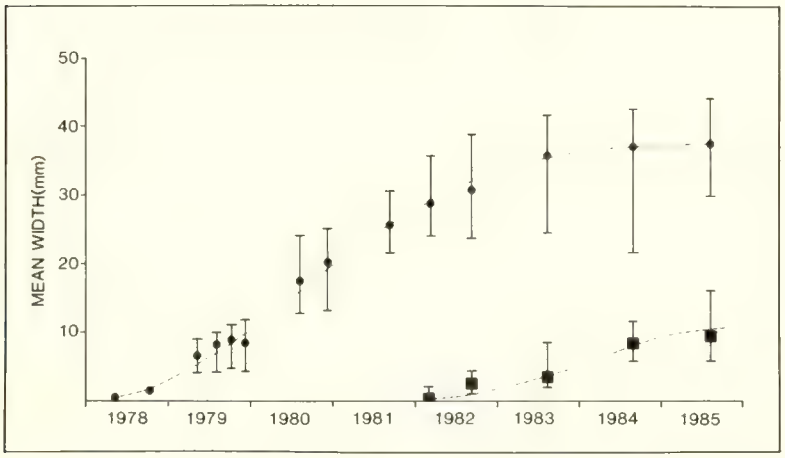

Figure 7
Growth curves from the shift of the mean widths and ash-free dry-weight values of the prominent 1977–78 *Echinarachnius parma* cohort, over time, at station 15A, Middle Atlantic Bight.

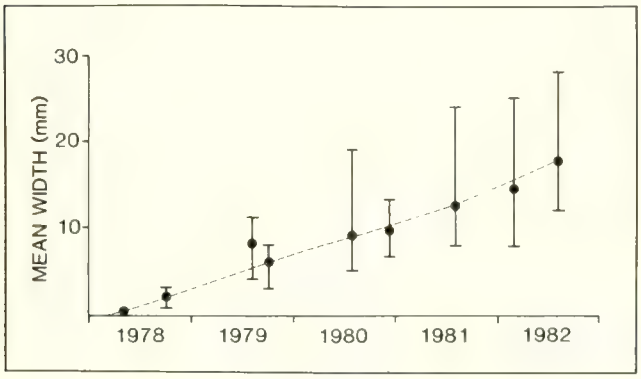

Figure 8
Growth curves from the shift of the mean widths of the prominent 1978 *Echinarachnius parma* cohort, over time, at station 23, southwestern Georges Bank.

Table 1
Mean estimates of *Echinarachnius parma* growth rate, based on cohort-size modal shifts at three stations in the Middle Atlantic Bight and southwestern Georges Bank.

Station	Cohort	Approx. mean growth rate (mm/yr)
17	1976–77	6.0
	1977–78	4.5
15A	1977–78	5.5
23	1978	4.0

estimated cohort age (Fig. 9), based on the modal progression analysis or estimated growth rates, for all stations combined produced a skewed normal curve.

Discussion

The population dynamics of *E. parma*, with variable annual recruitment and cohort survival patterns (Figs. 2–5), are in general agreement with population dynamics reported for other echinoderms (Ebert and Dexter 1975, Lane and Lawrence 1980, Ebert 1983, Beukema 1985). Recruitment is evident as peaks in the 0–2 mm size-frequency columns of Figures 2–5. Station 17 (Fig. 3) was the exception, however, to the almost annual or frequent recruitment pattern; detectable recruitment was evident there in only 2 years. This recruitment pattern may be associated with anoxic conditions that defaunated this area during the summer of 1976 (Steimle and Radosh 1979). The definition of the first definable cohort at this station in July 1977 included some animals larger (to 12 mm) than the 6-mm estimated maximum annual growth rate, although the size-frequency mode was about 6 mm for the initial July 1977 collection (Fig. 3). It must be assumed any preanoxia recruitment in 1976 did not survive the event, as few living *E. parma* were found in the area

Table 2

Estimates of annual cohort production and P:B ratios for *Echinarachnius parma* and total annual population production and P:B at all stations in the Middle Atlantic Bight and southwestern Georges Bank. Production (P) values are mg ash-free dry weight (AFDW)/ m^{-2} · year, and biomass (B) values are mg AFDW. Conversions to energy equivalents are based on a mean conversion of 24 KJ/g AFDW (5.74 Kcal/g AFDW) (from Steimle and Terranova 1985).

Station/ annual period	Cohort 1972–73?			Cohort 1976–77			Cohort 1978–79			Cohort 1979–80			Cohort 1981–82			Total P/m^2		
	P	B	P:B	P	B	P:B	P	B	P:B	P	B	P:B	P	B	P:B	mg AFDW	Kcal	P:B
Station 11																		
Nov–Oct																		
1977–78	184	1217	0.15	21	71	0.30										205	1.18	0.16
1978–79	599	2843	0.21	270	208	1.30	180	94	1.91							1049	6.02	0.31
1979–80	781	717	1.09	1004	810	1.24	952	541	1.75	30	10	3.00				2767	15.88	1.34
1980–81	211	2288	0.09	102	429	0.24	611	848	0.72	170	185	0.92	9	345	0.03	1103	6.33	0.27
1981–82				369	697	0.53	974	722	1.35	371	344	1.08	14	9	1.56	1728	9.92	0.98
1982–83				179	518	0.35							2	1	2.00	181	1.04	0.35
																$\bar{X}$ = 1172	6.72	0.57
	Cohort 1976–77			Cohort 1977–78														
Station 17																		
1976–77	802	667	1.19													802	4.60	1.19
1977–78	1556	1092	1.42	310	101	3.07										1866	10.71	1.56
1978–79	2967	1420	2.09	1479	1523	0.97										4446	25.52	1.51
1979–80	3405	4707	0.72	4675	3564	1.31										8080	46.38	0.98
1980–81	1632	6072	0.27	5305	5534	0.96										6937	39.82	0.60
1981–82	2801	7054	0.40	2796	27870	0.10										5597	32.13	0.16
																$\bar{X}$ = 5068	29.09	0.94
	Cohort 1972–74?			Cohort 1977–78			Cohort 1978–79?			Cohort 1979–80?			Cohort 1980–81					
Station 15A																		
1977–78	−13	1584	−0.01	49	13	3.77										36	0.21	0.02
1978–79	−65	1936	−0.03	550	556	0.99										485	2.78	0.19
1979–80	−58	4554	−0.01	2369	965	2.45	86	44	1.95							2397	13.76	0.43
1980–81				1887	2404	0.78										1887	10.83	0.78
1981–82	−65	2403	−0.03	1927	5092	0.38				218	27	8.10	239	101	2.37	2319	13.31	0.30
1982–83	53	1362	0.04	371	14960	0.02							202	25	8.10	626	3.59	0.04
																$\bar{X}$ = 1292	7.41	0.29
	Cohort 1976–77			Cohort 1977–78			Cohort 1978–79			Cohort 1979–80			Cohort 1980–81					
Station 23																		
May–April																		
1978–79				27	8	3.39										27	0.15	3.39
1979–80	70	107	0.65	83	84	0.99										153	0.88	0.80
1980–81	246	353	0.70	310	377	0.82	30	9	3.33	7	06	1.17				593	3.40	0.80
1981–82	466	579	0.80	1019	1327	0.77	40	41	0.98	23	3	7.67	2	2	1.00	1550	8.90	0.79
1982–83	236	1838	0.13	1178	3131	0.38										1414	8.12	0.28
																$\bar{X}$ = 747	4.29	1.21

during the fall of 1976. These few were found at sites, nearby, that were on the tops of sand ridges near or in the thermocline, offering less anoxia-stressed conditions (Steimle and Radosh 1979). This suggests there may have been accelerated growth of some recruits spawned in nearby areas unaffected by anoxia, possibly a response to a rich detrital food supply remaining from the related phytoplankton bloom (Mahoney and Steimle 1979) and an absence of competitors or predators.

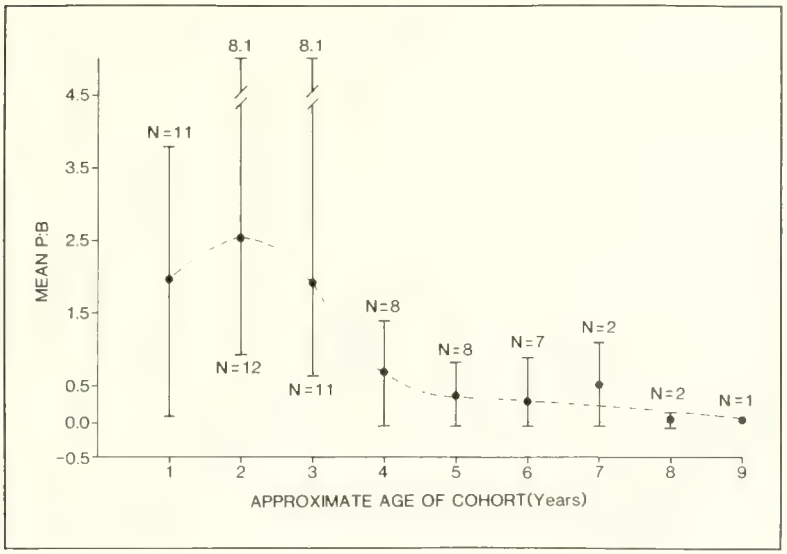

Figure 9

Relationship between production (P) to biomass (B) ratios (mean and ranges) and estimated age for all definable *Echinarachnius parma* cohorts from all stations, Middle Atlantic Bight and Georges Bank.

The period of peak recruitment varied slightly between the Middle Atlantic Bight stations and that of Georges Bank. Recruitment was heaviest or most consistent in the winter to early spring (December–April) at Stations 11 and 15A (Figs. 2, 4) which is consistent with most reports of fall *E. parma* spawning (Fewkes 1886, Cocanour and Allen 1967, Ruddell 1977). Recruitment of the two cohorts found at Station 17 (Fig. 3) occurred prior to when sampling began, but the 1978 cohort was probably recruited in the winter of 1977–78. On Georges Bank (Fig. 5), however, recruitment appeared in all collections except those of September, and most did not persist. Collie's (1987) observation of yellowtail flounder selectively feeding on <12 mm size *E. parma* on Georges Bank is relevant to the poor survival of most new cohorts there.

The life span for persistent cohorts in the Middle Atlantic Bight, estimated from recruitment in 1976 to the end of the study, was at least 7–8 years, e.g., see Figure 3. The presence of a few larger individuals, to 54 mm, suggests a maximum life span of perhaps 15+ years, given the probable very slow growth rates of the larger/older segment of the population. However, maximum widths were generally below 40 mm which suggests that most of the population did not live much more than 8 years. At the Georges Bank station, recruitment prior to the 1978 cohort was not evident, thus reasonable estimates of maximum size, life span, or other population variables were not possible because collections there covered less than 5 years.

The estimated life span of *E. parma* in the study area is most likely less than the estimated 21 years reported by Brykov (1975) for a Pacific population of this disjunctly trans-subboreal species, based on assumed annual growth-ring counts to estimate age. However, individuals of *E. parma* have been measured that generally exceed 80 mm (maximum reported is 92 mm) in the northern Gulf of Maine (Lohavanijaya 1964, Cocanour 1969), and if one uses a mean growth rate of about 3 mm per year (range 1.5–4 mm/year) as determined from tagged, middle-sized (33–55 mm) individuals measured after 2 years in the Gulf of Maine (Cocanour 1969), then 20+ year life spans could occur in boreal waters. If annual ring counts to size estimates of Cocanour (1969) alone were used, it appears a lesser age would be reasonable because 60–70 mm animals had only 6–7 growth rings. The reduced growth rates of a cohort as it reaches senescence may not produce distinguishable growth rings and juvenile rings may also be weak or obscure, so ring counts could underestimate age. Also, Cocanour (1969) has suggested that mature *E. parma* may alternate years of growth and gametogenesis, at least in the Gulf of Maine; there is no evidence of this alternate-year growth pattern in the growth curves (Figs. 6–8). The maximum width measured in the Middle Atlantic Bight was 54 mm. This apparent difference in maximum size, and possibly life spans, between populations in the temperate Middle Atlantic Bight and the boreal Gulf of Maine suggests a latitude or temperature-related size cline for this species, as predicted for echinoids in general by Ebert (1975). Other factors, e.g., food supply, genetic variability, differences in methodologies, or habitat or predation pressure, could also be involved.

Although the collection periods caused some problems in accurately defining the specific time of peak recruitment, the quarterly-to-semiannual sampling over at least the initial 5-year period of the study was probably sufficient to estimate growth and production. Parsons et al. (1977), for example, suggest the

sampling period for growth and production estimates should be no greater than 10% of the generation time (from egg to sexual maturity) of a species. Ruddell (1977) reports *E. parma* reaches sexual maturity at a width of about 27 mm in the Middle Atlantic Bight. This width suggests an age of approximately 5 years from the growth curve at Stations 17 and 15A (Figs. 7 and 8); thus, semiannual sampling appears to meet this suggested minimum.

The slightly sigmoidal growth curves, for most prominent cohorts (Figs. 6–8), differ from the more parabolic growth curves reported for other sand dollar species (Ebert and Dexter 1975, Lane and Lawrence 1980) and sea urchins (Ebert 1982). However, Sime and Cranmer (1985) and Nichols et al. (1985) report sigmoidal growth curves in North Sea echinoid species. Some of the irregularities in growth curves in the present study may be due to a sigmoidal, intra-annual, seasonal growth cycle that would have highest rates in the early summer and lowest in the early winter (Cocanour 1969). These curves, based on defined cohort means, may be somewhat imprecise because of the small sample sizes; however, the modes are basically congruent with the means and support the general shapes of the curves. The apparent growth curves for Stations 17 (1976/77 cohort, Fig. 6) and 15A (1977/78 cohort, Fig. 7) are almost congruent although the Station 17 (1977/78) cohort has a lower slope, similar to that of the Station 15A (1981/82) cohort or that of the Station 23 (1977/78) cohort curve. The cause of difference in these two sets of slopes is unknown, at present.

The mean annual growth rates (Table 1), estimated by modal progression analysis, ranged from 4.0 to 6.5 mm per year and were greater than the average 1.5–4.0 mm per year rates reported by Cocanour (1969), based on tagged individuals, for an intertidal population along the northern Maine coast. However, the ratios of number of apparent growth rings to diameter were generally higher, ranging from about 7.5 to 15 mm per ring. The rates estimated in the present study are less, however, than the approximate 7 mm per year from Woods Hole, Massachusetts (Durham 1955) or the 7.5 mm per year off northern New Jersey (Graef 1977), both determined by growth ring counts for 45–48 mm specimens. The diameter-to-ring ratio ranged from 4.3 to 11.3 mm per ring for eight smaller specimens in Graef's study and appeared to peak at about 34 mm with three rings evident. The size range examined by these two studies is near the predicted size asymptote, and senescence may be involved with zero or negative growth which would underestimate the age and overestimate overall growth rates. Negative growth (shrinkage), evident as slope declines on the right side of curves found for some older cohorts, agrees with similar findings by Cocanour (1969) for this species and for other sand dollars (Lane and Lawrence 1980). Senescence is thought by these authors to be the cause of this negative growth in older populations, although Gordon (1929) and Cocanour (1969) report some shrinkage in all age classes during winter months. There is better agreement between the growth-ring count estimates and the size-frequency estimates of growth rate if it can be assumed that the relatively slow juvenile growth, suggested by the sigmoid growth curves and reported by Gordon (1929) and Highsmith and Emlet (1986) for a Pacific population, may leave an obscure ring for the first or perhaps even second year of survival, thus lowering the size-age estimates based on ring counts. On Georges Bank, the most persistent or dominant cohort was the 1978 recruitment. The growth patterns (Fig. 8) suggest a mean growth rate of about 4 mm per year for the first 4 years of this cohort, although there was some irregularity in July 1979. This rate is slightly lower than most rates for similiar cohorts at other stations.

The overall, estimated annual cohort and population production varied from station-to-station and from year-to-year (Table 2), reflecting the variable dynamics of recruitment, growth, and mortality of each population. It is interesting to note that population production peaked in the November 1979–October 1980 production year at all three Middle Atlantic Bight stations and later, during the May 1981–April 1982 production year for Georges Bank. The *E. parma* population at Station 17 was the most productive for the period examined, and its total production peaked in 1979–80 at 8080 mg AFDW/m^2 per year This production level (46 Kcal/m^2 per year), when converted to energy equivalence (24 KJ or 5.7 Kcal/g AFDW; Steimle and Terranova 1985), is greater than the total benthic community production reported in many North Atlantic continental shelf areas (table 5, Steimle 1985); even the mean value for this station, 29 Kcal/m^2 per year is comparable to some total community values. The high production at Station 17 is probably related to the 1976 anoxia episode, mentioned previously.

The P:B ratios (Table 2) varied from negative values for older cohorts to a maximum of about 8.1 for some juvenile cohorts at Station 15A. A comparison of mean cohort P:B ratios against approximate cohort age (Fig. 9) for all stations combined shows a skewed normal curve, with mean ratios per age group ranging from a maximum of about 2.4 for 1–2 year-old cohorts to less than 0.5 for cohorts older than 5 years. The declining part of this curve appears to be common in other marine organisms, e.g., Warwick (1980). The low P:B ratios for 0–1 year-old cohorts could suggest a relatively slow growth of young-of-the-year juveniles (Figs. 6–8). The apparently low initial ratios could also be influenced by accurately establishing time of recruitment.

Table 3
Summary of production (P) to biomass (B) ratios for some echinoderms.

Class Species	P:B (range)	Reference
Holothuroidea		
Cucumaria elongata	0.26	Zaika (1972)*
Echinoidea		
Strongylocentrotus droebachiensis	0.80	Miller and Mann (1973)
Echinocardium cordatum	(−0.002–3.7)	Warwick et al. (1978)
Brissopsis lyrifera	0.30	Buchanan and Warwick (1974)
Moira atrops	0.82–1.0	Moore and Lopez (1966)
Echinarachnius parma	(0.02–3.39)	Present study
Stelleroidea		
Astropecten irregularis	0.005	Warwick et al. (1978)
Asterias forbesi	2.64	Richards and Riley (1967)
Asterias rubens	(3.6–7.3)	Zaika (1972)*
Ophiura albida	0.84	Arntz (1971)
Ophiura texturata	0.68	Warwick et al. (1978)
	0.48	Warwick and George (1980)
Amphiura filiformis	1.97	O'Connor et al. (1986)
Amphioplus coniortode	2.26	Moore (1972)
Amphipholus squamata	1.8	George and Warwick (1985)
Ophiothrix fragilis	1.8	George and Warwick (1985)
Ophionepthys limicola	2.33	Moore (1972)
Amphiodia arctica	(0.6–0.8)	Zaika (1972)*)

*Ratios calculated from published data.

Mean P:B ratios for *E. parma*, although generally declining with the age of the cohort (Fig. 9), are comparable to the range of P:B ratios determined for other echinoderms (Table 3). Because of the variable relationship of P:B ratios to the (1) specific population age structure (Fig. 9), (2) segment of the life span, or (3) other factors, the significance of this comparison is uncertain. This problem has attracted the attention of other authors who have attempted to improve the utility of interspecific comparisons of P:B ratios by scaling them to either temperature (Parsons et al. 1977), body mass at maturity (Banse and Mosher 1980), or life span (Winberg 1971, Zaika 1972).

The results could be affected by a number of sources of error or variability that commonly affect similar studies and are usually difficult to assess, e.g., sampling error. We did not have samples near the end of the presumed winter-spring peak of larval settlement to obtain accurate estimates of the time and density of larval recruitment. This could affect the growth curves or production estimates. The production of any missed recruits during the few weeks or months before they were sampled would probably be minor because of their small size and high mortality rate. It could influence the cohort P:B-to-age curve (Fig. 9) and partially explain the initial low ratio and rise. Later, semiannual sampling also made it difficult to determine if *E. parma* spawns more than once per year. There are suggestions of substantial recruitment outside of the approximate peak periods (or delayed recruitment) in some of the histograms, especially for the Georges Bank station (Fig. 5).

Another source of error may be systematic, e.g., annual mean production or P:B values do not adequately consider a cyclic annual growth and production patterns. These appear to have maximum values in the warmer months, based on the study of Cocanour (1969), when specific rates would be much higher than the mean annual values.

The final source of error is statistical, especially considering the small sampling sizes available to estimate many of the variables, e.g., the size mode of each cohort. The relatively long time series of data examined, however, allowed a better definition of cohort size modes and growth than is normally possible by attempts to interpret a limited number of collections over a short time and reduced the necessity for alternate aging estimates.

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Abstract.—Pacific herring *Clupea pallasi* eggs were collected from spawning grounds in Bristol Bay, Alaska, transferred to Norway for hatching, and for 63 days raised in a 2000-m^3 marine basin located at the Flødevigen Biological Station. The eggs were from the same spawning, and hatching took place over 3 days. Upon completion of hatching, 24,840 larvae (12.42 larvae/m^3) were released into the basin. Larval growth was rapid and metamorphosis was observed 28 days after hatching at a length of 25 mm. The experiment was terminated by draining the basin; 4891 juveniles were recovered. The average rate of growth was 0.66 mm/day in length and 2.89 mg/day in weight. The larval length frequency, unimodal at hatching, segregated into three modes within 2 weeks, which persisted until termination. The slowest growth rate was 0.31 mm/day and the larger herring averaged 1.48 mm/day. At first feeding, copepod nauplii were abundant but food declined later. Cannibalism was observed on day 45 and a 30-mm herring was captured that contained a 20-mm herring. Survival was higher in the basin than estimated for larvae at sea. Mortality appeared to be greatest during the first 2 weeks, and much of it may have been due to hydromedusa predation.

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Observations on Growth and Survival During the Early Life History of Pacific Herring *Clupea pallasii* from Bristol Bay, Alaska, in a Marine Mesocosm

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Pacific herring *Clupea pallasii* that spawn in northern Bristol Bay are the largest herring off western North America and are genetically distinct from herring in the Gulf of Alaska and off British Columbia (Fried and Wespestad 1985, Grant and Utter 1984) (Fig. 1). Very little is known of the early life history of Bristol Bay herring. Checkley (1982) examined otoliths from age-0 juveniles for growth increments and sampled post-hatching larvae at several spawning areas in western Alaska (Checkley 1983). These studies provided limited information on early growth, since the time of spawning and hatching were unknown and otolith increments were not verified to be daily rings.

To investigate the growth in length and weight of larval and post-larval Bristol Bay herring and other aspects of early life history, known-age herring were sampled from hatching to postmetamorphosis in a marine mesocosm. A mesocosm study was chosen because larval density could be regulated as well as sources of mortality, such as predators and food supply which cannot be done in a field study. Control of these variables is possible in a laboratory experiment, but Øiestad (1983) has shown that container size may bias laboratory results. He investigated the early life history of Atlanto-Scandia herring *Clupea harengus* and the effect of ration and predation on survival in a large marine enclosure located at the Flødevigen Biological Station near Arendal, Norway. The results of his studies showed life history parameters of herring in the basin were similar to those observed in nature.

Methods

Herring eggs on rockweed (*Fucus* sp.) were collected at low tide on 24 May 1986 from a single spawning that occurred on 22 and 23 May. Water temperature at the time of spawning was 4.5°C and salinity was 30 ppt. *Fucus* fronds with light egg coverage (1–2 egg layers) were collected at random within the spawning area and packed into half-liter plastic bags filled with seawater. A total of 25 bags were filled with about 2000 eggs per bag. The bags were shipped via air in insulated containers with gel ice to the Flødevigen Biological Station. After 48 hours in transit, the eggs were unpacked and placed in hatching boxes supplied with circulating seawater at 7.7°C and salinity of 32 ppt.

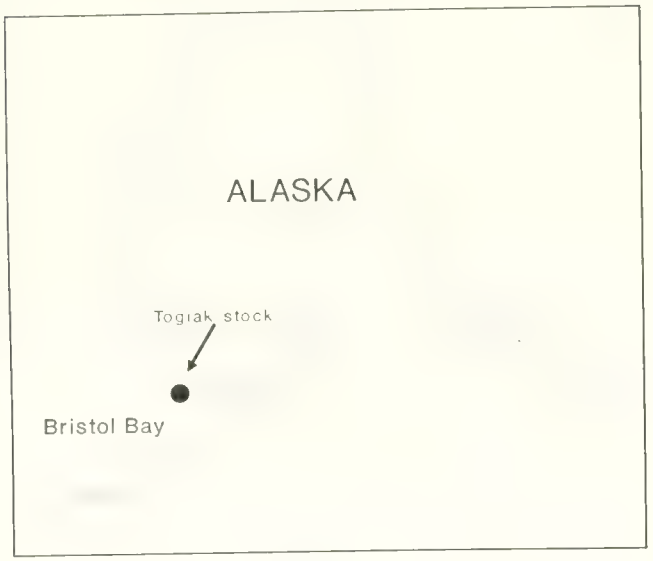


Figure 1
Location of spawning grounds of the Togiak herring stock in Bristol Bay, Alaska.

Hatching began on 10 June 1986 and was completed by 12 June. Survival to hatching was about 50%, with 25,200 larvae produced. The eggs were not treated during incubation, and heavy fungal growth was noted on the eggs. Newly hatched larvae were collected from incubation boxes in white plastic cups in groups of 5–25, counted, and transferred to 5-L cylinders placed in an 8.1°C water bath. Each cylinder held 1000 larvae.

On 13 June, 24,840 larvae were released into a large outdoor basin (2000 m^3 volume, 600 m^2 surface area, maximum depth 4.0 m) filled with seawater pumped from Flødevigen Bay. Phytoplankton and zooplankton abundance was high when the larvae were introduced to the basin. A detailed description of the basin is presented in Moksness (1982).

Larvae were retained in the laboratory to examine starvation-induced mortality. Four batches of 100 larvae were placed in 5-L cylinders supplied with filtered seawater. Temperature was maintained at 8°C by placing the cylinders in a water bath. A batch was terminated every 7 days and the larvae recovered and preserved with buffered 4% formalin.

The larvae in the basin were sampled daily using a two-chambered plankton net of 500-μm mesh and a total sampling area of 0.3 m^2. The net was drawn diagonally across the basin at a depth of 2 m. The total volume sampled was 7.5 m^3. Larvae and invertebrates captured in the plankton nets were preserved in buffered 4% formalin for later analysis.

Weekly estimates of zooplankton density were obtained from pump samples taken from depths of 0.5, 1, 2, and 3 m. Water was pumped from each depth for a short period prior to filtering a 30-second sample through a 90-μm plankton net. Samples were preserved in 4% formalin and examined later using a binocular microscope and counting chamber. Temperature, salinity, and oxygen saturation were measured at each depth on the day pump samples were obtained.

Preserved larvae were examined using a binocular microscope vernier eyepiece; they were measured, examined for food contents, and weighed. Length was measured from the snout to the tip of the notochord in larvae, and to the hypural plate in postlarvae. To test for shrinkage due to preservation, a sample of 21 newly hatched larvae were anesthetized, measured, and then preserved in 4% formalin. After 10 days the larvae were measured. The live length, 7.70 mm (SD 0.42), and the preserved length, 7.74 mm (SD 0.35), were not different. Under the preservation conditions employed, shrinkage of about 8% would be expected based on results presented by Hay (1982).

For food examinations, the entire gut was removed from post-yolk sac larvae. After the stomach differentiated, it was removed for food content analysis. After gut or stomach removal, larvae were placed on Teflon strips and dried at 60°C for 24 hours and then weighed using an electronic balance.

Results

Environmental parameters

The Flødevigen Biological Station is located at 58°24′N which is approximately the same latitude as the herring spawning ground in Bristol Bay (59°00′N), so herring in the basin experienced the same daylength as they would in Bristol Bay. The temperature in the basin averaged 11.75°C when the larvae were introduced on day-0, 3 days after hatching (Fig. 2a). Initially the basin was at a nearly uniform temperature varying from 11.9°C at the surface to 11.6°C at 3.5 m. After the larvae were introduced, temperatures in the basin began to rise owing to a prolonged period of sun and above-average air temperature. On day-12, surface temperature reached 18.8°C and then declined to range between 14 and 16°C for the remainder of the experiment. Temperatures below 2 m increased but not as sharply as surface waters (Fig. 2a). For the duration of the experiment, temperatures averaged 15.2, 15.1, and 15.8°C at 1, 2, and 3+ m, respectively. Temperature data recorded on the same dates offshore of the Bristol Bay spawning grounds at a depth of 2 m show that the temperatures in the basin averaged 4.5°C higher (15.26°C vs. 10.7°C).

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Salinity during the experiment ranged from 30.6 to 32.7 ppt (Fig. 2b). The lowest salinity values were recorded at the start of the experiment followed by a slight increase throughout the experiment. The increase in salinity was attributed to evaporation and in flow of a small amount of denser water pumped into the basin to offset losses from evaporation and leakage.

Oxygen levels were checked periodically during the experiment. The lowest levels were recorded on day-12 at 70% saturation. At other times oxygen saturation was near 100%.

Zooplankton

Calanoid copepod adults and nauplii were the primary component of the zooplankton in the basin, constituting 26% and 68% of the number of organisms in pump samples, respectively (Fig. 3a). Adult copepod abundance was greatest when the herring larvae were introduced into the basin; it then declined rapidly (Fig. 4a). Copepod nauplii were also at greatest abundance in the beginning and declined over time from a peak of over 100/L to less than 1/L (Fig. 4b).

The other plankton species taken in pump and net samples were present at much lower densities (Fig 4c). The non-copepod zooplankton were primarily harpacticoid copepods, *Littorina littorea* veligers, crab (*Cancer pagurus*) zoea, and cladocera (*Bosmina* sp., *Evadne* sp., and *Podon* sp.). *Ephyra* sp. hydromedusa were abundant in the first days of sampling and then declined rapidly.

Feeding

Herring larvae in the basin fed primarily on copepod eggs, nauplii, and adults (Fig. 3b). Other items found in the diet were *L. littorea* veligers, crab zoea, and chiromomid larvae which occurred in the basin sediments. Food items were found in the gut within a few days of release into the basin. Within the first 5 days of release, 12% of the larvae contained food items (Table 1).

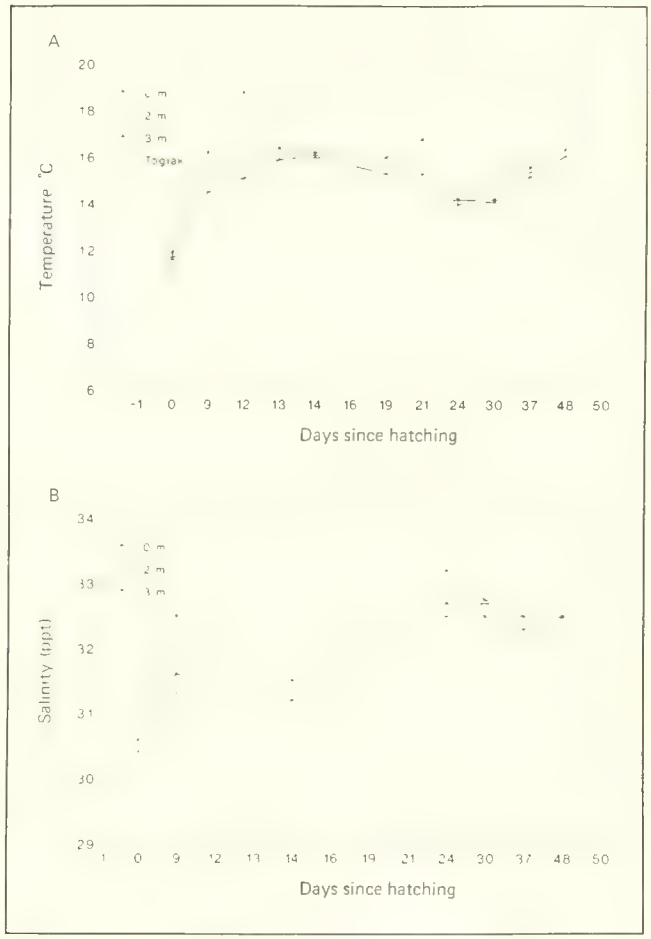


Figure 2

(A) Water temperature in the 2000-m^3 basin, Fløedevigen Biological Station, Norway, at 0, 2, and 3 m compared with observed temperature at 2 m in Togiak Bay, Alaska. (B) Salinity (ppt) in the 2000-m^3 basin at 0, 2, and 3 m.

The items observed in the gut during the first week were primarily copepod nauplii and eggs. The proportion of larvae with food doubled in the second week; eggs and nauplii continued to be major items, but small copepods were also found (Table 1). From day-13 to

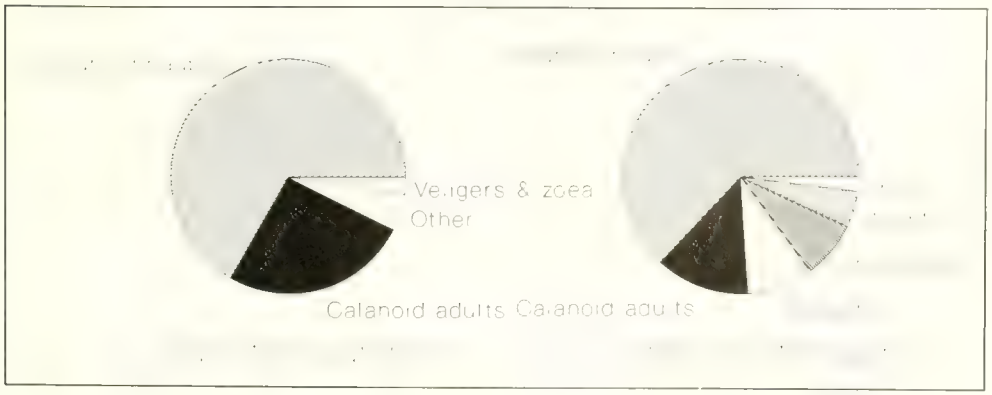
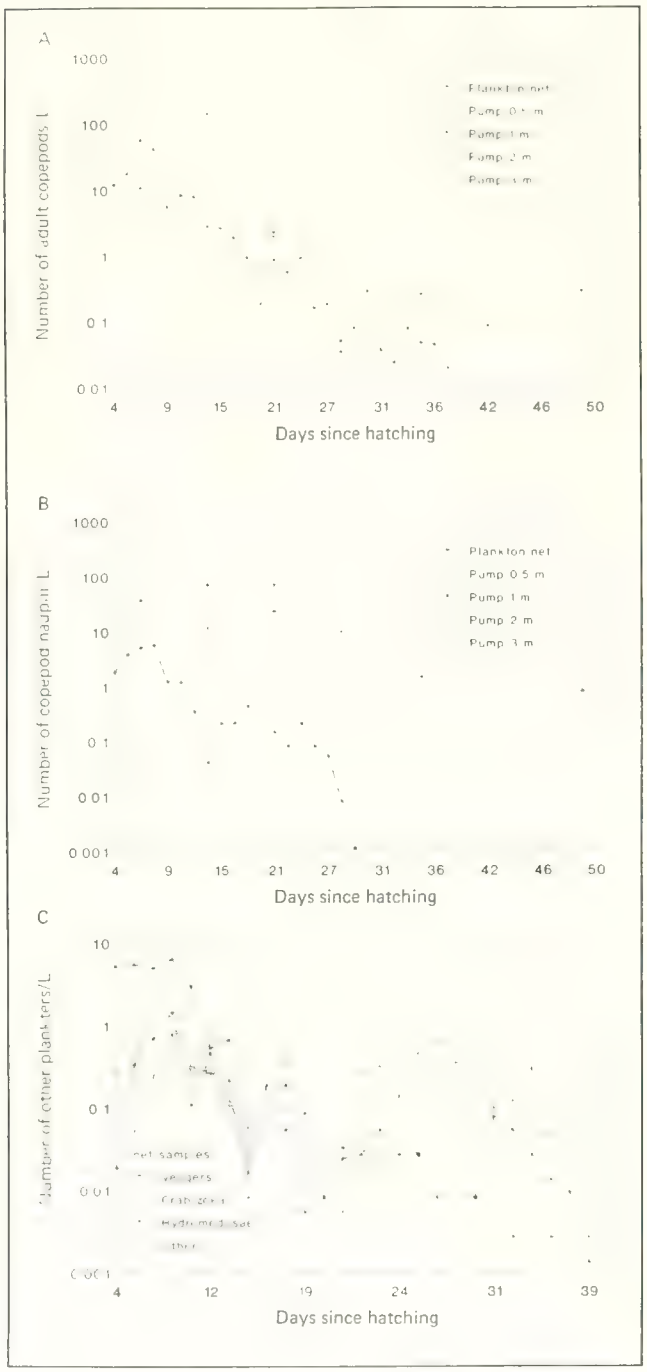


Figure 3

Comparison of (a) species composition in plankton samples and (b) food items consumed by Pacific herring larvae.



day-21 the herring captured did not contain food items. This may have been due to regurgitation during capture, or the larvae may not have been feeding immediately prior to capture. The absence of food is likely a combination of the shock of capture and preservation, two processes which have been shown to cause significant voiding of the gut (Rosenthal 1969, Hay 1981).

By day-22 the stomach had begun to differentiate, and greater than 75% of the larvae had food items in the stomach from this time forward. The frequency of copepod eggs and nauplii occurrence decreased and adult copepods increased; also, other items appeared in the diet, primarily veligers and crab zoea.

On day-43 cannibalism was observed in the basin. On that date a school ($N = 10$) of 60–80 mm herring was observed attacking schools ($N = 10$–60) of smaller herring. Immediately afterward, dip net samples were attempted and two herring, one 57 mm and the other 32 mm, were obtained. The 32-mm herring was found to contain a 20-mm herring.

Comparison of feeding relative to abundance, using the Ivlev (1961) electivity index, shows that adult copepods were increasingly selected as the herring grew and that copepod nauplii were less utilized (Table 2). Veligers and crab zoea were not utilized initially but were strongly selected after the larvae had grown large enough to consume these species.

Growth

The average length of newly hatched larvae was 7.61 mm (SD 0.53), average dry weight 190 μg (SD 38.5) and yolk volume 0.16 mm^3 (SD 0.09) (Table 3). Measurements were taken of herring hatched each day and no significant differences were found between days (F test, $\alpha = 0.05$).

Figure 4

(A) Number of calanoid copepods/L, (B) number of calanoid copepod nauplii/L, and (C) number of hydromedusae and other plankton/L in net samples in the 2000-m^3 basin, Fløddevigen Biological Station, Norway.

Table 1

Proportion of Pacific herring from Bristol Bay, Alaska, containing food and percentage of major food items consumed during five time-periods.

		Items consumed					
		Copepods					
Day	Percent with food	Nauplii	Adults	Veligers	Diptera	Crab zoea	Unidentified
2–5	12	95	5	0	0	0	0
8–12	23	83	17	0	0	0	0
13–21	0						
22–27	77	66	12	13	1	9	0
29–35	81	47	13	9	15	11	4

Table 2
Electivity index (Ivlev 1961) of Pacific herring larvae from Bristol Bay, Alaska, for items found in plankton and stomach samples by time periods.

Days	2–5	8–12	13–21	22–27	29–33
Copepods					
adults	−0.61	0.04	—	0.64	0.50
nauplii	0.10	0.01	—	0.19	−0.13
Veligers	−1	−1	—	0.71	0.77
Crab zoea	−1	−1	—	0.82	0.53

Table 3
Average length, weight, and yolk volume at hatching of Pacific herring larvae from Bristol Bay, Alaska. Standard deviation in parentheses.

Date	*N*	Length (mm)	Weight (μg)	Yolk volume (mm^3)
11 June	50	7.46 (0.68)	180.48 (52.01)	0.19 (0.10)
12 June	25	7.74 (0.35)	218.00 (30.48)	0.17 (0.12)
13 June	24	7.77 (0.43)	181.33 (19.58)	0.09 (0.03)
Total		7.61 (0.53)	190.07 (38.52)	0.16 (0.09)

The length of newly hatched herring was normally distributed with length ranging from 6 to 9 mm (Fig. 5a). The distribution of weight was skewed slightly, and dry weight ranged from 91 to 300 μg (Fig. 5b).

The length at hatching of these larvae is similar to that reported from other Pacific herring stocks: British Columbia 4–8 mm (Stevenson 1962), 8.5–9 (Alderdice and Hourston 1985); California 8 mm (Talbot and Johnson 1972.)

The growth rate from hatching to experiment termination 63 days later averaged 0.66 mm/day and ranged from 0.31 mm/day for the smallest to 1.48 mm/day for the largest. Daily growth increased from 0.1 mm/day on day-3 to 0.64 on day-21 and then decreased (Fig. 6a).

A Gompertz growth curve

$$L_t = L_\infty e^{-k \cdot e^{-bt}},$$

was fitted to the length-at-age data, where

L_∞ = Length infinity
k = Brody growth coefficient
b = regression constant
t = age in days.

The resulting parameters were L_∞ = 202.3 mm (SD 86.34), k = 3.299 (SD 0.389), and b = 0.013 (SD 0.03). The fit of observed length to the model is shown in Figure 6b. The poor fit is due to the lack of observations beyond the inflection point. Based on the length of age-0 herring captured in the Bering Sea in September, L_∞ should be between 80 and 90 mm and k proportionately lower.

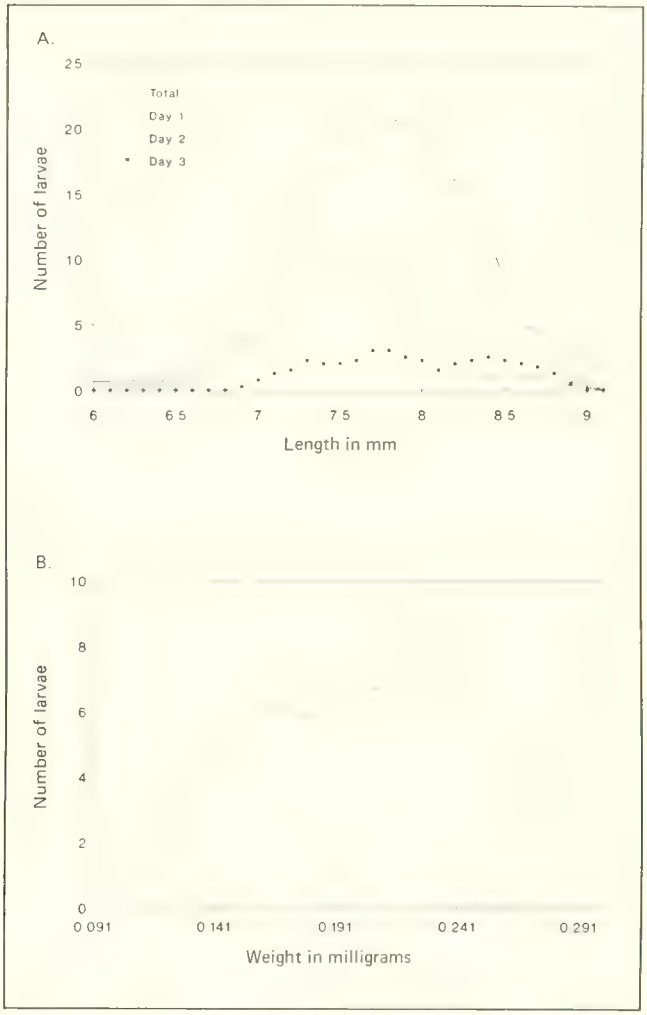


Figure 5
(A) Length-frequency and (B) weight-frequency distribution at hatching of Pacific herring larvae from Bristol Bay, Alaska.

Weight-at-age was more variable than length-at-age (Fig. 6c). Average weight increased in weight from 0.19 mg at hatching to 182 mg on day-63, or an average daily growth rate of 2.89 mg/day. The specific growth rate,

$$\ln(\text{wt})_i - \ln(\text{wt})_0 / t_i - t_0$$

where $\ln(\text{wt})$ = $\log_e$ weight,
t_i = day i,
t_0 = day 0,

exhibited a decrease as yolk was depleted and then increased to a peak on day-21, which was followed by a decline similar to daily growth in length (Fig. 6a).

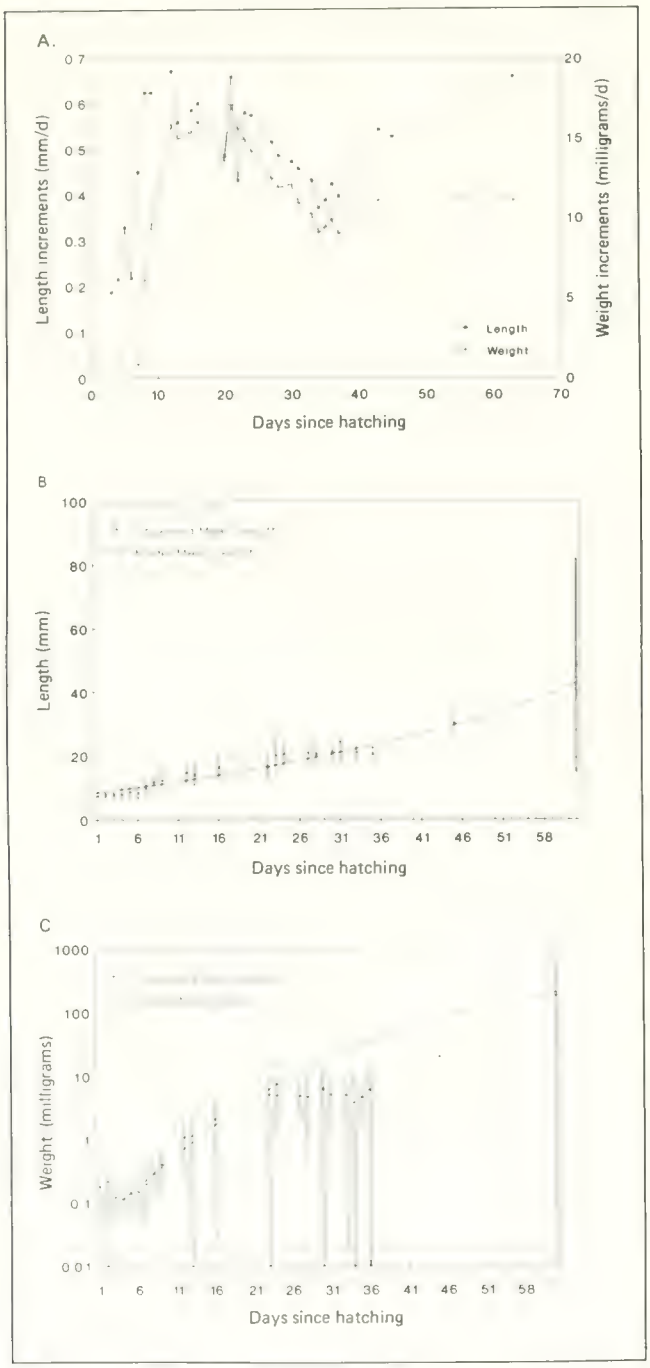


Figure 6

(A) Growth increments in length (mm/d) and weight (mg/d) for Pacific herring from Bristol Bay, Alaska, in a 2000-m^3 basin at Flødevigen Biological Station, Norway. (B) Observed length-at-age and 95% confidence interval, and length-at-age estimated by a Gompertz model (solid line), of Pacific herring in the basin. (C) Observed weight-at-age (mg) and 95% confidence interval, with a Gompertz model growth estimate, of Pacific herring from Bristol Bay, Alaska, in the 2000-m^3 basin at Flødevigen Biological Station, Norway.

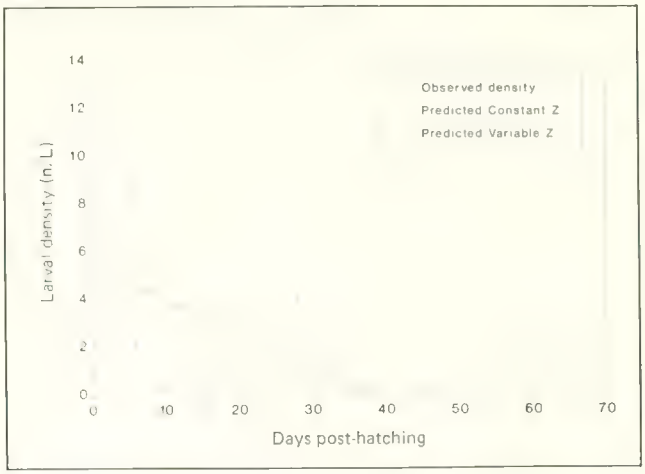


Figure 7

Estimated survival of Pacific herring from Bristol Bay, Alaska, in the 2000-m^3 basin at Flødevigen Biological Station, Norway, from yolksac stage to termination on day-63, based on plankton net samples fit to constant and variable mortality (Z) models.

The great variability in weight made it difficult to fit a growth model by nonlinear least-squares. A modified Gompertz model (Zweifel and Lasker 1976) was examined iteratively by fixing one parameter and varying the others. The Gompertz model and observed weights are shown in Figure 6c. It can be seen that the model describes growth well to day-25, but then observed growth deviates from predicted growth. The point of deviation is at the time metamorphosis commences, when the more robust fish may have begun to avoid the sampling net. Ware (1975) points out that net avoidance often results in underestimation of growth rate.

Survival

Of the 24,840 larvae released into the basin, 4891 were recovered when the basin was drained on day-63. The overall survival rate in the basin was 19.69%, total instantaneous mortality (Z) = 1.625. The daily mortality rate was 2.7%.

Comparison of the estimated density (fish/m^3), based on decay of the initial population by the daily mortality rate, with the density of larvae estimated from plankton net samples shows that net samples underestimated larval abundance in the basin if the rate of decline was constant (Fig. 7). The net samples suggest that mortality was initially high following release and then declined. A two-part mortality curve is shown in Figure 7 which estimates daily mortality to be 15.08% during day-3 to day-12 followed by a rate of 0.05% for the remainder of the experiment.

Table 4

Summary of larval survival of Pacific herring from Bristol Bay, Alaska, held without food. Standard deviation in parentheses.

Day	No. alive	Sample size	Mean length (mm)	Mean weight (μg)	Mean yolk volume (mm^3)	Condition factor (K)
1	100	25	7.0 (0.1)	175 (29)	0.101 (0.04)	52.2 (0.07)
8	88	25	9.4 (0.2)	147 (27)	0.004 (0.01)	18.0 (0.03)
13	93	25	9.1 (0.1)	119 (26)	0	15.7 (0.02)
19	52	25	9.0 (0.3)	109 (20)	0	15.5 (0.03)

Table 5

Growth rates reported for Pacific herring *Clupea pallasii* larvae.

Growth rate (mm/d)	Days	Temperature (°C)	Location	Source
0.48–0.52	15	8.9–9.1	BC1	Alderdice and Hourston 1985
0.40–0.80	30?		BC2	Stevenson 1962
0.39–0.79	30	8.0–14.0	WA	Keegen et al. 1986
0.33	60	9.0–12.0	CA	Talbot and Johnson 1972
0.78–0.94	87		BB	Checkley 1982
0.60	100	11.0–16.0	JN	Mority 1985

BC1 Strait of Georgia, British Columbia; **BC2** Barkley South, British Columbia; **WA** Northern Puget Sound, Washington; **CA** laboratory, San Francisco Bay, California; **BB** Bristol Bay, Alaska; **JN** Hokkaido, Japan.

Herring held in the laboratory and deprived of food died 21 days after hatching. Larval survival was high until day-19 at which time the number alive had decreased to 52% (Table 4). Mortality proceeded rapidly at this point, and total mortality was observed in the remaining batch on day-21 of the experiment.

Length increased in starved herring during the first week from an average of 7.0 mm to 9.4 mm and then remained essentially unchanged for the remainder of the experiment (Table 4). Weight, on the other hand, decreased from 175 μg on day-1 to 147 μg near the end of the yolksac stage and to 109 μg on day-19 (Table 4).

Discussion

The development of Bristol Bay herring larvae in the basin was similar to that reported for other stocks. The average growth of 0.66 mm/day was near the upper end of the range reported from British Columbia and Washington but greater than that observed in aquaria experiments in California (Table 5). Direct comparison is difficult because of the differences in duration of observation periods, but it is likely that the 0.33 mm/day reported for San Francisco Bay herring is low due to a diet of *Artemia* nauplii, which have been shown to produce poorer growth than natural plankton (Blaxter and Hunter 1982).

Comparison of our results with otolith ring data (Checkley 1982) indicates that the growth observed in the basin is similar to at-sea growth. The otolith-ring age estimates were 0.78 mm/day and 0.94 mm/day for herring of 82 mm average length and 108 mm maximum length. These are likely slight overestimates of growth rates since there is a lag time between hatching and ring formation related to yolksac absorption (Messieh et al. 1987, Moksness and Wespestad 1989).

McGurk (1984) concluded that growth in laboratory experiments is always lower than at-sea growth. The similarity between growth rates observed in the basin and rates estimated from at-sea otoliths suggests that the basin environment resembled natural conditions. Stevenson (1962), Keegen et al. (1986), and McGurk (1984) reported higher growth rates for batches of larvae developing at higher temperature.

Blaxter and Hunter (1982) relate that the growth rate of herring is primarily governed by temperature and food abundance. In Bristol Bay, summer surface-water temperatures are warmest nearshore (10°C and greater) and decrease (7°C or less) a short distance offshore (Ingraham 1981). That herring growth in the basin was similar to growth observed in field samples

suggests that, in Bristol Bay, herring larvae are retained in the nearshore zone during the larval period to experience a temperature regime similar to that observed in the basin. Herring larvae transported out of coastal waters would develop in much colder water and exhibit a reduced rate of growth.

The mortality of larvae in the basin was high during the first 2 weeks of the experiment, with daily mortality estimated to be as high as 14%. This is about one-half that estimated for a wild population observed over a 20-day period in which daily mortality was 32% (Stevenson 1962). The higher survival in the basin is consistent with the results of Moksness and Øiestad (1987), who estimated daily mortality to be higher (4%) for the first 30 days and then much reduced (0.8%) to day-100 for Atlantic herring in the same basin.

The higher initial mortality of Pacific herring in the basin may be due to predation. Hydromedusae known to consume herring were abundant during the first week Pacific herring were in the basin. In the experiment with Atlantic herring, the occurrence of hydromedusae was much later, beyond day-40. Arai and Hay (1982) estimated that hydromedusae predation in British Columbia could account for a daily larval loss of 9%.

Starvation may not have been a significant source of mortality because the abundance of copepod larvae, the preferred food of herring larvae, was much higher at the time of first feeding of Pacific herring than was estimated at the same point for Atlantic herring (Moksness and Øiestad 1987). Kiørboe et al. (1985) report that herring are able to successfully initiate feeding at prey densities much lower than usually present in the sea at the time of first feeding.

Cannibalism may have been an important source of mortality in late-stage larvae. Blaxter and Hunter (1982) report that cannibalism has been observed in situations in which a size hierarchy has developed, although they believe this is a rare occurrence based on the scarcity of reports of cannibalism in aquarium studies. However, the observation of attacks on smaller herring in this study suggests that cannibalism was not a rare event in the basin population. Cannibalism may have been related to the reduced abundance of zooplankton at the time it was observed. However, fish larvae may be a normal component of the diet of post-larval herring since capelin *Mallotus villosus* larvae were rapidly consumed by newly metamorphosed herring in an earlier basin study (Moksness and Øiestad 1987). Also, Hourston et al. (1981) reported that age-1 Pacific herring, 71–91 mm standard length, readily consumed larval herring when placed together in a 197-L tank.

An interesting aspect of herring growth in the basin was the development of three distinctive length modes

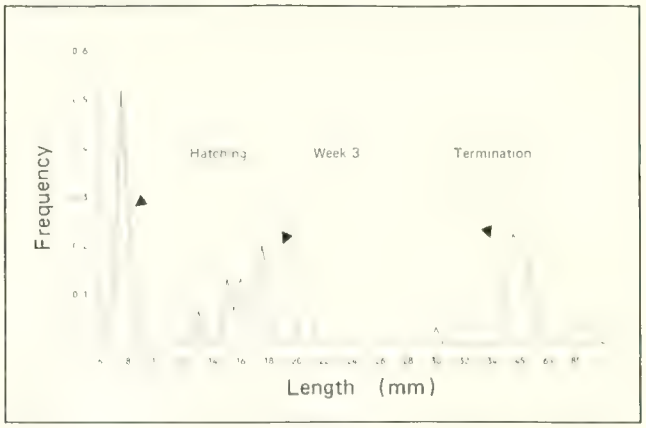


Figure 8
Length-frequency distribution of Pacific herring from Bristol Bay, Alaska, in the 2000-m^3 basin at Flødevigen Biological Station, Norway, at hatching, week-3, and study termination on day-63.

from an essentially unimodal population at hatching (Fig. 8). The cause of distinct size modes in this experiment is unknown, but it may be related to success at first feeding or be genetically based, because size differences developed early.

Blaxter and Hunter (1982) report that strong size hierarchy has been observed in some aquarium studies of herring, which they speculate may involve crowding or food competition; however, in a previous study of Atlantic herring larvae in a 4400 m^3 basin a size hierarchy did not develop (Øiestad and Moksness 1981). McGurk (1984) found that length and weight of larvae of the same hatch differed at 30 days posthatch as a result of withholding food from 0 to 14 days. This suggests that modes may be a reflection of feeding success. Moksness et al. (1989) observed that in ocean catfish differences in feeding success at first feeding was expressed as differential growth that persisted throughout the larval period.

Although most of the literature suggests that differential growth is related to early feeding success genetic factors may also influence larval growth and survival. Christopher et al. (1988), in a study of capelin *Mallotus villosus* larvae from known females crossed with a single male, found that the amount of yolk varied among the females and that growth and survival was correlated with yolk quantity.

Whatever the cause, one would tend to conclude that the modes were distinct "cohorts" from different hatchings if observed in the wild. The significance of these results is that a method such as otolith daily ring counts is required to validate larval age and the use of length-frequency analysis to determine the occurrence of cohorts may lead to erroneous assumptions. If differential growth among a brood is a common

occurrence in nature, it may complicate analyses and results of larval cohort studies such as those of Lambert (1984).

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Hyperostosic Bones from the New Zealand Snapper *Chrysophrys auratus* (Sparidae)

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General hyperostoses are well known in fossil fish bone literature (Tiffany et al. 1980). Hyperostosic bones have been described as occurring as nodules on the ventral pterygiophores as well as other bones of Recent fishes (Olsen 1971, Fierstine 1968, Konnerth 1966). Consistent occurrence of hyperostosic bones in many species has been taken to indicate that they are not pathological (Fierstine 1968).

Various roles have been suggested for hyperostosic bones ranging from aids in fin erection (Fierstine 1968) to hydrostatic correction (Breder 1952). The hydrostatic suggestion arose from the observation that hyperostosic bones are "filled with fat" (Breder 1952), and oils in fish bones have been proposed as an aid to neutral buoyancy (Lee et al. 1975). Hyperostoses in sparids of the genus *Chrysophrys* have also been used as characters to separate *Pagrus major* from *Chrysophrys auratus* (Yasuda and Mizuguchi 1969).

Hyperostosic bones occur in the snapper *Chrysophrys auratus* and are usually highly vascularized. We were interested in (1) the possible relationship between size of hyperostosic bones and fish size and (2) the significance of the fatty-acid composition of hyperostoses to the biology of the fish.

Materials and methods

Snapper were measured as fork length, filleted along one side to reveal the hyperostosic bones, and photographed on a measuring board. The hyperostosic bones and a sample of the vertebrae from each fish were dissected out and frozen at −15°C until the fat content was analyzed. The relative sizes of hyperostosic bones were measured from the photographs. Two hyperostosic bones usually occur in the snapper, commonly on the seventh (preural) haemal spine and less commonly on the sixth haemal spine from the tail in specimens of the size range (31–48 cm) used in this study. Both were measured. The eighth and ninth vertebrae from the tail were removed and analyzed as nonhyperostosic comparisons.

One bone was cut through the hyperostosis, mounted in epoxy resin, and ground down to about 50-μm thickness and photographed with a WILD M400 stereomicroscope. Whole fish were x-rayed using a Faxitron Model 804 Radiographic Inspection Unit. Ten of the specimens examined were aged from the otoliths using an annual check-ring method (Paul 1976).

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Flesh and connective tissues were scraped off the bones. Prior to chopping, bones bearing the hyperostoses were cut diagnoally. Bones were weighed, chopped into small pieces, and extracted three times with chloroform-methanol (2:1 v/v) in an ultrasonicator bath (Sanophon Ultrasonic Ind.) containing iced-water for 10 minutes and finally extracted once with chloroform. The extracts were combined, filtered, and evaporated at 40°C in a rotary evaporator and weighed. Extracted lipids were stored under nitrogen at −15°C pending analysis.

Fat-free bone residues were dried to constant weight. The lipid extract is expressed as a percentage on a dry matter basis (Table 1). Lipids were separated into classes by column chromatography and preparative thin-layer chromatography. All solvents used were redistilled prior to use. Portions of total lipids dissolved in chloroform were initially separated into fractions on 30 g and 12 g columns (depending upon sample sizes) packed with silica acid (Koch–Light Lab. 5024h, 100–200 mesh) previously activated at 110°C. The elution procedure involved chloroform for neutral lipids and methanol for polar lipids. By combination of silicic-acid column chromatography and preparative thin-layer chromatography, neutral lipids were resolved into their constituent categories (Tables 1, 2).

Preparation of methyl esters and gas-liquid chromatography (GLC) was carried out in the following way. Aliquots of total lipid extracts, which contained fatty acids combined as glycerides and phospholipids, and transesterified with BF_3-methanol (Van Wijngaarden 1967). Fatty-acid methy esters were analyzed by GLC using a Pye Unicam GCV and a Philips PU 4500 capillary chromatograph fitted with flame ionization detectors. Both

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Table 1

Hyperostoses (H) and vertebrae (C), extraction and column chromatography in *Chrysophrys auratus*.

	Fish 1		Fish 2		Fish 3		Fish 4		Fish 5		Fish 6		Fish 7		Fish 8		Average values	
	H	C	H	C	H	C	H	C	H	C	H	C	H	C	H	C	$\bar{H}$	$\bar{C}$
Total lipid extract																		
Weight (mg)	17.4	4.2	58.9	34.7	24.4	12.0	31.4	12.3	16.3	8.6	37.3	12.2	7.3	5.5	51.4	49.4		
% (dry matter basis)	3.11	4.57	16.91	17.73	11.50	10.71	2.04	5.10	6.96	8.14	22.70	16.90	8.00	14.29	29.30	22.93	12.57	12.55
Column chromatography (%)																		
Triglycerides	58.0	57.1	58.4	58.1	58.2	57.2	58.0	57.7	58.3	58.1	58.4	48.2	58.9	58.2	58.6	58.5	58.35	57.89
Sterols and alcohols	29.9	30.9	30.9	30.6	30.6	30.0	30.6	30.9	30.7	30.2	30.0	30.3	30.1	30.9	30.0	29.9	30.35	30.46
Total neutral lipids	87.9	88.0	88.9	88.6	88.6	87.5	88.6	88.6	89.0	88.3	88.4	88.5	89.0	89.1	88.6	88.4	88.63	88.38
Total polar lipids	9.8	9.5	10.7	10.1	10.2	10.0	10.2	10.6	10.4	10.5	9.6	10.6	9.6	10.6	10.1	9.9	10.08	10.23

Table 2

Fatty acid composition of the lipids of hyperostoses (H) and vertebrae (C) (expressed as percentage of GLC peak areas) in *Chrysophrys auratus*.

	Major components as fatty acid methyl esters										
	Fish 1		Fish 2		Fish 3		Fish 4		Fish 5		Snapper fillet**
	H	C	H	C	H	C	H	C	H	C	
Saturated											
14:0	4.1	4.4	3.9	4.2	5.8	6.3	5.1	4.7	4.3	3.8	4.4
15:0	0.8	0.7	1.0	0.8	0.7	0.7	0.8	1.0	0.8	0.9	1.0
16:0	35.9	34.2	31.2	28.0	27.8	26.8	28.5	27.9	35.1	30.8	36.1
17:0	0.9	0.9	0.9	0.9	1.0	1.0	0.9	1.0	0.8	0.8	0.8
18:0	10.9	11.2	11.4	11.0	11.2	12.4	12.0	11.6	11.0	12.6	11.3
Other	0.3	0.7	0.4	1.9	4.4	0.8	1.9	2.8	0.3	1.1	0.9
Total saturated	52.9	52.1	48.8	46.8	50.9	48.0	49.2	49.0	52.3	50.0	54.5
Unsaturated											
16:1 ω_7*	7.9	8.3	8.5	10.4	7.9	6.6	8.4	9.2	8.5	7.9	6.7
16:3 ω_4	0.9	1.0	1.2	1.4	0.9	2.5	1.5	1.2	0.9	1.0	0.8
18:1 ω_9	22.1	21.8	24.9	25.0	21.9	20.9	23.2	21.8	23.0	24.8	22.2
18:2 ω_6	1.0	1.3	1.9	1.0	1.2	2.1	1.6	1.4	2.0	1.7	0.8
18:3 ω_3	2.9	2.6	2.1	1.9	2.9	2.6	2.4	2.2	2.9	2.5	0.6
20:1 ω_9	1.5	1.6	1.0	1.0	2.0	2.2	1.6	1.6	1.0	1.6	1.2
20:4 ω_6	1.7	1.7	1.3	0.5	1.0	1.5	1.1	1.4	1.2	1.1	2.1
20:4 ω_3	1.2	1.9	1.2	1.5	1.3	1.7	1.4	1.6	1.7	1.5	0.2
20:5 ω_3	0.9	1.1	1.9	1.5	2.2	1.9	1.9	2.0	2.1	1.8	0.3
22:5 ω_6	1.0	0.8	1.1	1.1	0.8	1.2	1.1	1.0	0.9	1.0	1.3
22:5 ω_3	0.8	0.7	0.7	1.1	1.1	1.3	1.0	1.2	1.0	1.2	1.8
22:6 ω_3	1.2	1.4	0.3	1.4	0.8	1.1	0.9	0.7	0.4	0.7	1.5
Other	2.1	1.7	3.1	3.6	3.3	4.3	2.8	3.7	0.2	1.4	4.2
Total unsaturated	45.2	45.9	49.2	51.4	47.3	49.9	48.9	49.0	45.8	48.2	43.7
Total branched	1.9	2.0	2.0	1.8	1.8	2.1	1.9	2.0	1.9	1.8	1.8

*ω_1 position of double bond nearest to terminal methyl group.
**Fatty acid composition of snapper fillet reported by Hughes et al. (1980).

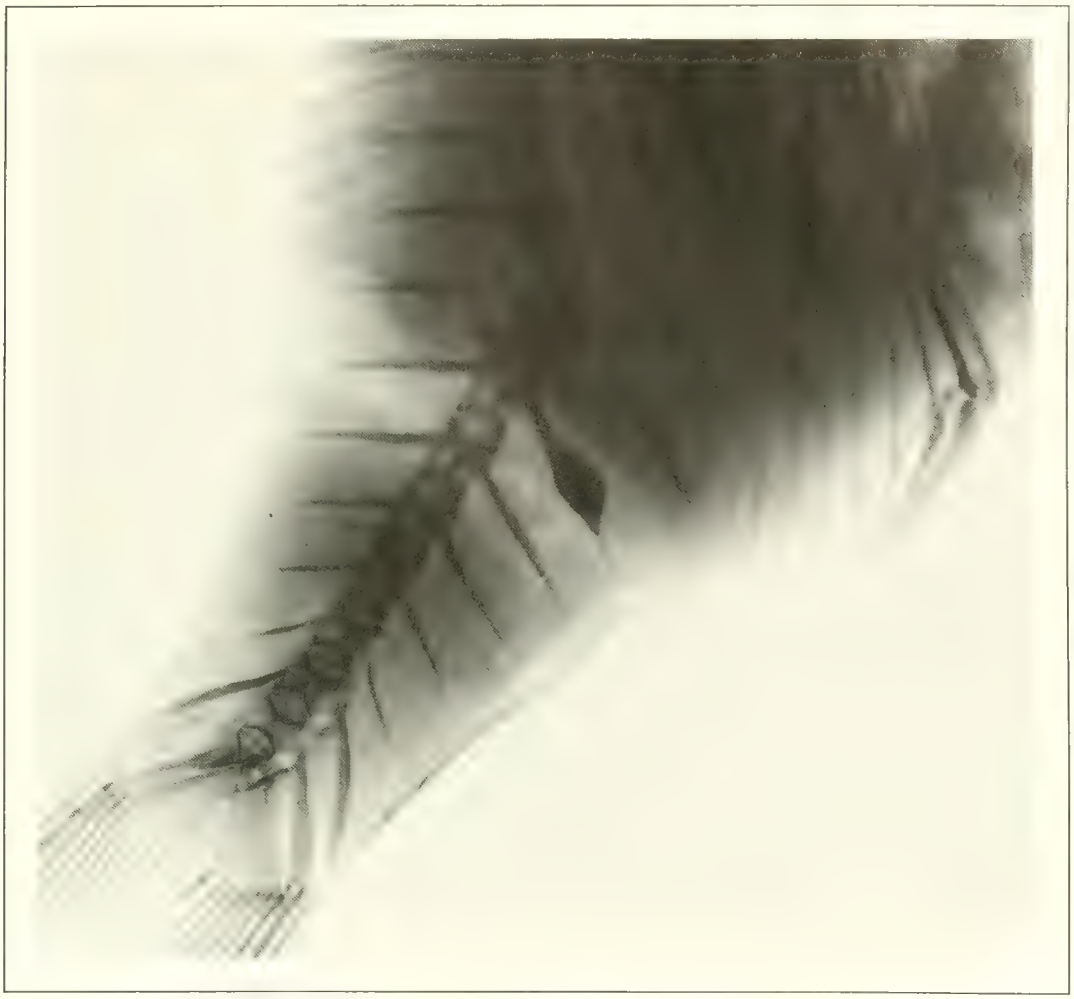

Figure 1
Radiograph of *Chrysophrys auratus* hyperostosic bones showing the enlarged haemal spines.

polar and non-polar columns were employed, the former containing 10% EGSS-X (210 × 0.254 cm i.d.) and the latter a BP-1 capillary column (25 × 0.33 mm i.d.).

Eight pairs of hyperostoses and vertebrae were analyzed (Table 1) for fat content and general fat composition. A subset of pairs of hyperostoses and vertebrae was used in the identifications of fatty-acid methyl esters based upon comparison of retention times with those of authentic reference methyl esters run under identical conditions. Where particular reference standards were not available, equivalent chain-length values reported by Hofstetter et al. (1965) and by Jamieson (1969) were accepted as criteria of identity. Identification was corroborated by hydrogenation of an aliquot of the esterified samples. Saturated and branched chain products were then analyzed by GLC on a polar column. The results of fatty-acid analyses were expressed as the percentage area occupied by each component methyl-ester peak relative to the total peak area. In the fatty-acid composition analyses reported here, the percentages were based on peak areas obtained with the 10% EGSS-X column (Table 2). Fatty-acid composition of snapper fillets (Hughes et al. 1980) is included for comparison in Table 2.

Results

Eight sets of snapper hyperostosic bones and controls were examined. An example of a pair of snapper hyperostosic bones is shown in Figure 1. In life, the hyperostosis has a reddish color and appears to be well vascularized. Commonly, hyperostoses occur both on the sixth and seventh haemal spine from the tail, as has also been described for *Chrysophrys unicolor* (Yasuda and Mizuguchi 1969). Although both hyperostoses may be enlarged, it is more common to find that the one

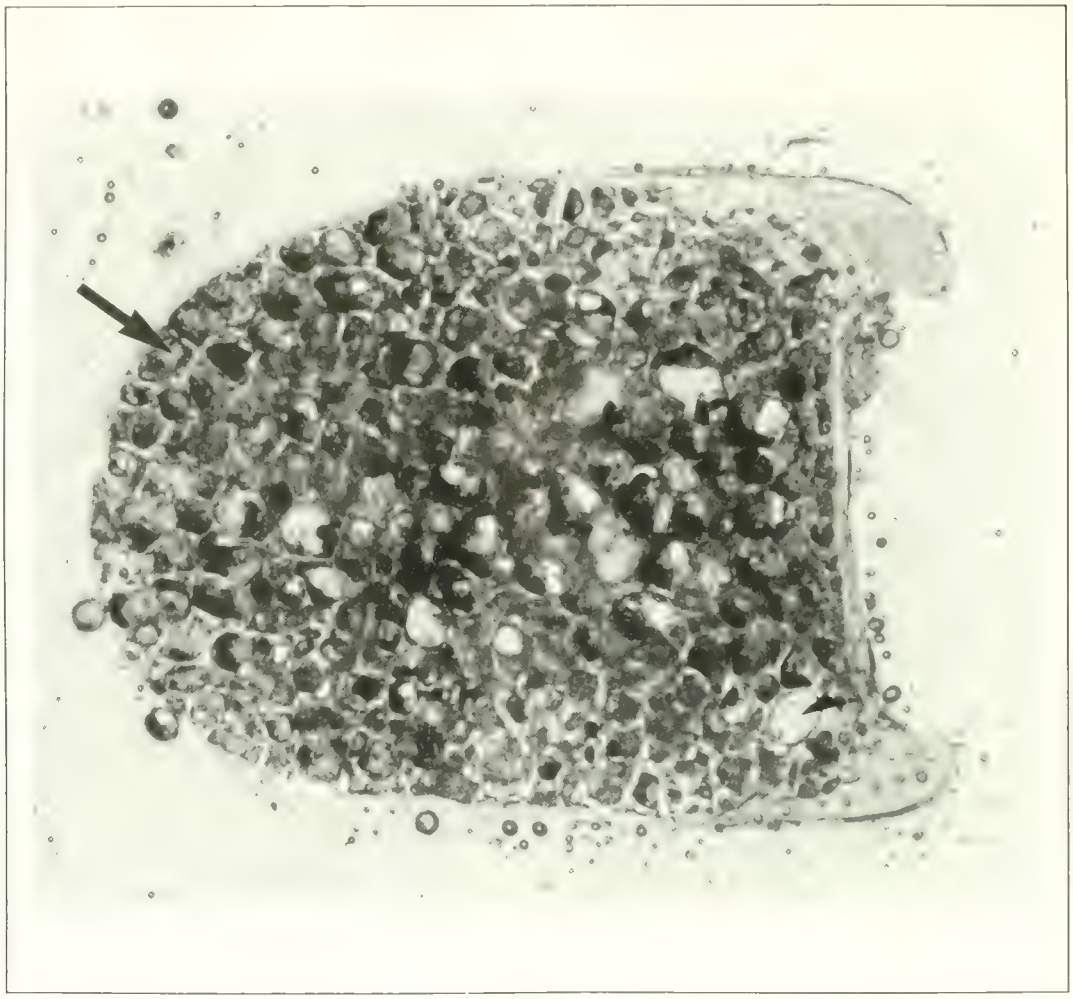

Figure 2

A section of a hyperostosic bone in *Chrysophrys auratus* shows a vacuolated structure (arrows) encased with bone

furthest from the tail shows less enlargement, as in Figure 1. Section of the snapper hyperostosic bone shows the vacuolated appearance (Fig. 2) characteristic of most fish bones.

The relative size of the most caudal hyperostosis was measured as the ratio of the width of the hyperostosis to the width of the spinal vertebra to which the haemal spine, on which the hyperostosis occurs, was attached. A plot of the ratio of hyperostosis width/vertebra width to fork length is shown in Figure 3. The correlation between relative size of the hyperostosis and fork length was low, $r = 0.58$. The correlation between the ratio of hyperostosis width/vertebra width to annual check-ring age was low, $r = 0.53$.

Eight pairs of hyperostoses/vertebrae were examined for fat content and fat composition (Table 1). The mean fat content of the hyperostoses (% dry matter) was 12.57 ± 19.34, and the mean fat content of vertebrae (% dry matter) was 12.53 ± 13.04. Although there was a certain amount of variation in fat content between hyperostoses and vertebrae, it was unlikely to be significant in any biological sense because fish lipid composition and content have been shown to be affected by diet to a greater extent than is shown in our data (Worthington and Lovell 1973).

The fatty-acid composition was almost identical ($\pm 5\%$) for all samples and very similar to the table presented in Love (1980: 414) for marine fish fatty-acid composition. A typical fatty composition for five pairs of hyperostoses and vertebrae is shown in Table 2. There was no significant difference in fatty-acid composition between the hyperostoses and vertebrae.

Discussion

Hypoerostosic bones of the snapper *Chrysophrys aurata* increased in size with increase in size of the fish,

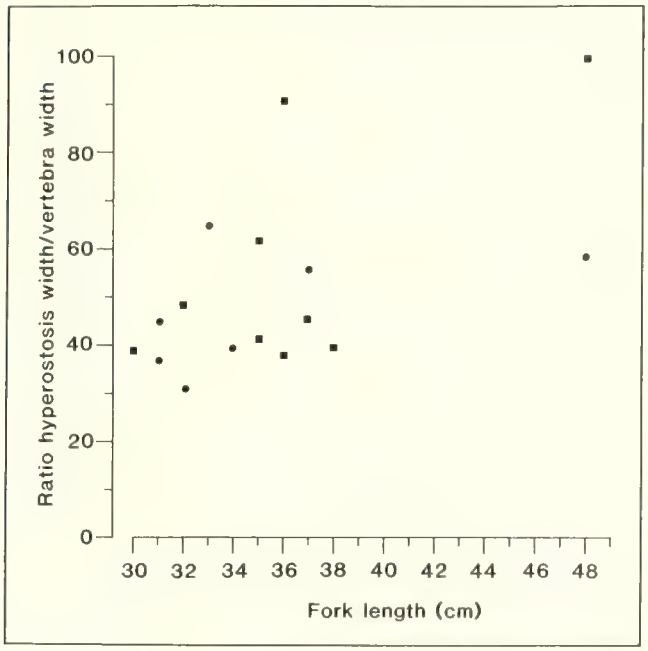

Figure 3
The ratio of hyperostosis/vertebra width in *Chrysophrys auratus* is plotted against fork length.

but the correlation between hyperostosic bone size and fish size was low. The relative size of snapper hyperostosic bones did not appear to be related with any more significance to age than to size.

The fat content of the snapper hyperostosic bones was not significantly different from that of the vertebrae. Nor was the composition of fat in the snapper hyperostosic bones significantly different from either the vertebrae of snapper or fats found in marine fishes generally. The difference in fat content between snapper hyperostosic bones and vertebrae is low (Worthington and Lovell 1973) compared with the potential range of differences in fat content known in fishes.

Snapper hyperostoses are vacuolated, but no more so than other bones in fish. The contribution of fat in hyperostosis to buoyancy is difficult to assess. The amount of lipid as a percent dry weight varies between individuals, but in some individuals is of the same order as the lipid content of the bones of fish species in which bone lipid may have a role in neutral buoyancy (Lee et al. 1975). However, the low correlation with both size and age suggests that if hyperostoses are related to buoyancy correction, then that relationship is tempered by factors other than size.

The use of hyperostoses to discriminate species both in Recent genera, such as *Chrysophrys* (Yasuda and Mizuguchi 1969) and fossil species (Fierstine 1968) points to another possible explanation. Hyperostoses occur with great regularity in certain bones in those species which display hyperostoses. We interpret such regularity as indicating that hyperostoses are under genetic control and are therefore good species characters, as are other genetically determined characters. But the expression of hyperostoses results from an indeterminate kind of ontogenetic process in which there is only a loose correlation between size of the hyperostoses and size or age. Thus the hyperostoses involve the local proliferation of cells (Breder 1952) but in a way that could be seen as physiologically between a normal bony growth and a bony tumor, almost a kind of controlled tumor which contains both fat cells and bony trabeculae. Snapper hyperostoses are readily obtainable and may provide a useful model to study the ultrastructural interactions between proliferating bone and fat cells.

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Gonad Morphology, Histology, and Spermatogenesis in South Pacific Albacore Tuna *Thunnus alalunga* (Scombridae)

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The reproductive biology of tuna, and the albacore *Thunnus alalunga* in particular, is not well understood with respect to functional morphology of the gonads in relation to sexual maturity. In the course of an investigation of the genetic variability of albacore, differences in morphology were observed between the right and left gonad of male and female fish and the size of the fat body associated with the gonads. Histological examinations were made to determine the relationship between these morphological differences and the reproductive state of the gonads. In this paper we report findings made on gonad morphology, histology, and spermatogenesis and relate them to the reproductive biology of this species.

Materials and methods

Albacore specimens were collected onboard the U.S. NOAA RV *Townsend Cromwell* and the New Zealand RV *Kaharoa* during cooperative studies conducted in 1986 and 1987 to investigate the biology/ecology and fishery exploration of albacore tuna in the South Pacific Ocean (Laurs 1986, Laurs et al. 1987). The fish were caught using standard albacore troll-fishing methods (Dotson 1980). In addition, specimens were collected during commercial fishing operations conducted in 1987 by Japanese longline vessels. Locations of specimen collection are summarized in Table 1.

Soon after the fish were caught, fork lengths were measured to the nearest millimeter and the gonads and associated fat body were dissected from each fish. The right and left gonads were preserved separately in 10% neutral buffered formalin. Histological preparations were initiated by washing the tissue in running water for 12 hours. An American Optical T/P tissue processor was used to dehydrate and embed the tissue in paraplast. The tissue was sectioned at 5 microns and stained with Harris' hematoxylin followed by eosin counter stain (Humason 1979, Gabe 1976).

Each testis subsample histological preparation was classified according to (a) estimates of the relative abundances of spermatocytes, spermatids, and sperm; (b) sperm-duct development; and (c) sexual maturity. In addition, the cross-sectional area of the medial section of each testis was determined. Electron micrographs were prepared of sperm, which had been washed from the sperm duct of selected testes with physiological saline and fixed in 3% gluteraldehyde in 0.1 M phosphate buffer.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

We observed asymmetrical differences in the size of both ovaries and testes and in the size of the fat body associated with gonads from both sexes of fish. Histological examination showed that all stages of sexual maturity were represented in the specimens of testes, allowing us to describe spermatogenesis. No sexually mature ovaries were found, limiting the results for females to asymmetrical size differences.

Number and size of fish examined

Gonads from 197 albacore were examined histologically during the study. Sex ratio was nearly 1:1, with 106 males and 91 females. The fish ranged in fork length (FL) from 50 to 101 cm. Over 90% of females and over 80% of males were less than 90 cm FL, the size at which sexual maturity is believed to first occur in female albacore (Ueyanagi 1955, Otsu and Uchida 1959, Otsu and Hansen 1961). Length-frequency distributions of the fish examined are given in Figure 1.

Gonad general morphology

As in most teleosts, the gonads in male and female albacore are paired, elongate organs, located in the dorsal portion of the body cavity. They

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Table 1

Summary of information on *Thunnus alalunga* specimens used in study.

Ship	Date	No. species	Fork length (cm) Range	Median	Location in South Pacific
RV *Townsend Cromwell*	1986 17–21 Feb.	33	50.6–84.4	71.5	Central lat. 38°–40°S long. 146°–152°W
RV *Townsend Cromwell*	1987 25 Jan.–1 Feb.	33	50.6–97.5	63.8	Central lat. 35°–39°S long. 151°–157°W
RV *Kaharoa*	1986 15 Feb.–28 Mar.	13	50.0–76.0	70.0	Western lat. 33°–44°S long. 166°E–178°W
FV *Wakashio*	1987 21 June	9	63.0–98.0	88.0	Western lat. 37°S long. 179°E
FV *Zuiho*	1987 20–23 June	18	85.2–101.1	94.5	Western lat. 37°–38°S long. 179°E

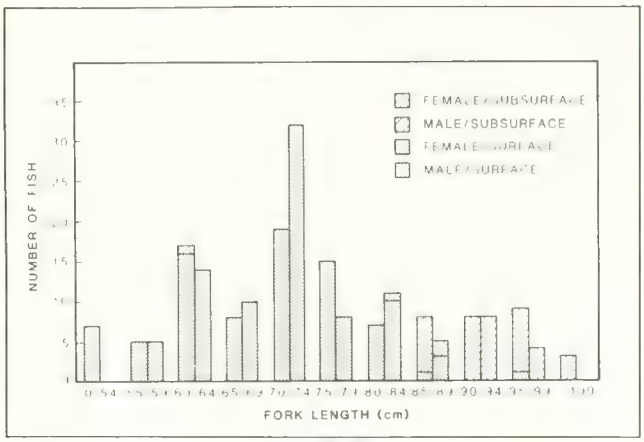

Figure 1

Length-frequency distributions for male and female South Pacific albacore tuna examined in this study. Surface troll-caught fish and subsurface longline-caught fish are differentiated.

are suspended by the mesentery which contains a fat body closely associated with the gonad between it and the dorsal body wall (Godsil and Byers 1944). The fat body will be discussed in a later section. Testes are thin and ribbon-like in immature fish, and develop into somewhat flattened, whitish-yellow organs which are relatively solid as the fish advance in maturity. Ovaries in immature fish closely resemble immature testes in appearance. They become progressively enlarged in length and girth and tend to be somewhat pinkish in color as the fish progresses in maturity.

We initially made casual observations, when collecting gonad tissue samples for genetic-variability studies of North Pacific albacore, that the right gonads were most often larger than those on the left side. The present study of nearly 200 South Pacific albacore showed that while right and left gonads of both sexes were about the same length, the cross-sectional area and volume of the right ovaries and testes were regularly larger than those on the left side. Figure 2 shows a pair of ovaries and associated fat bodies, portion of the digestive tract, and ventral fin dissected from a 94-cm FL North Pacific albacore. The disparity in size between the right and left ovaries and associated fatty bodies is typical of what we have observed in this study and in casual observations.

Size differences between right and left testes

Measurements of the cross-sectional area (mm^2) of the medial sections of the right and left testes provide quantitative estimates of size differences between the two. Data summarized in Table 2 show that the right testis was larger than the left in 72% of male fish examined, the two testes were equal in size in 2%, and the left was larger than the right in 23%.

The results given in Figure 3 show that the dissimilarity in size increases with increasing fork length. The right testis is about 28–32% larger than the left in fish less than 80 cm FL, but increases to about 66–75% larger in fish over 80 cm. Data on displacement volumes measured on a sample of the right and left testes showed results similar to those made on the measurements of cross section. Examination of relationships between fork length and cross-sectional area of the

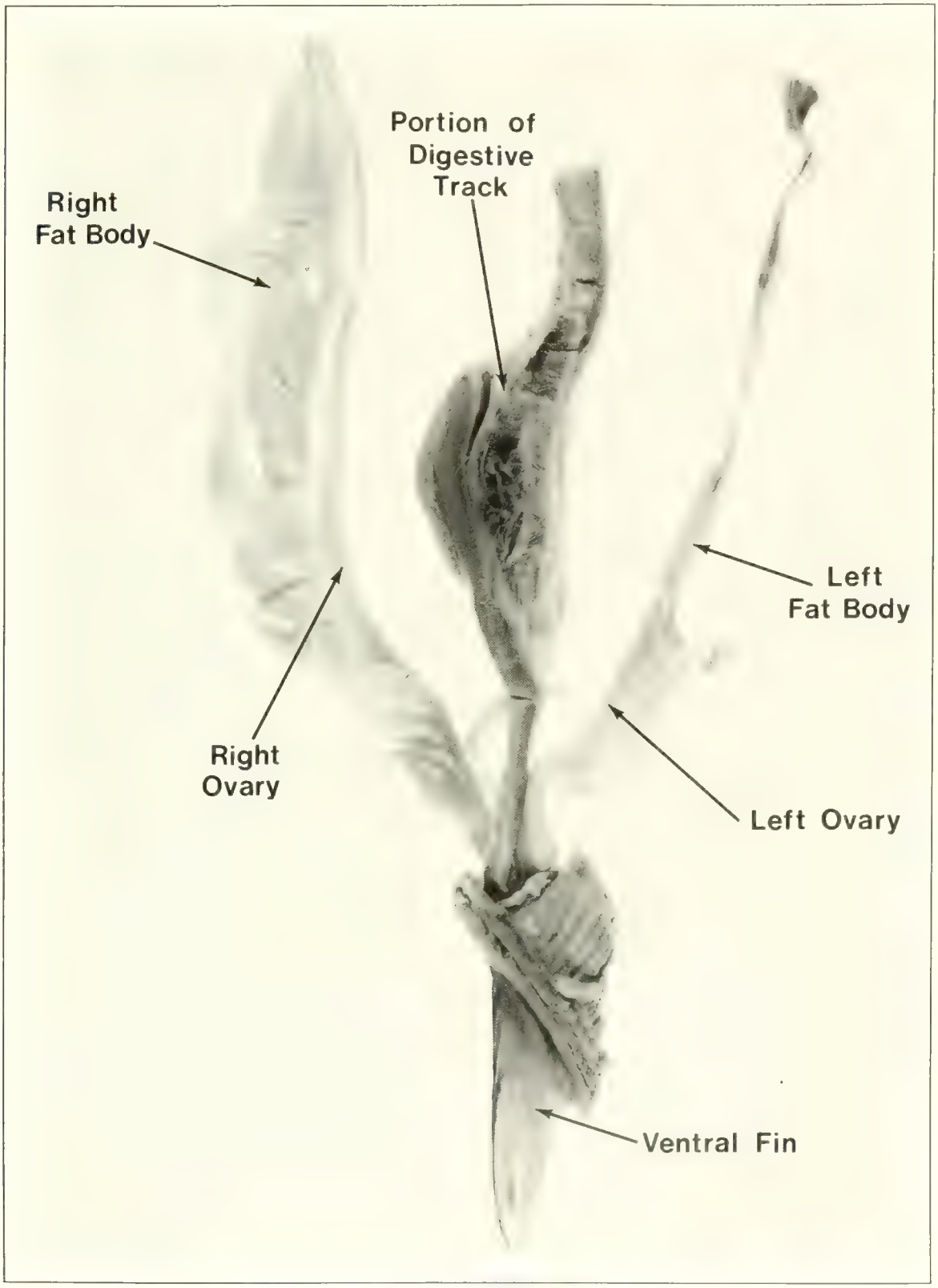

Figure 2

Pair of ovaries and associated fat bodies, portion of digestive system, and ventral fin from a 94-cm FL albacore tuna caught in the North Pacific.

Table 2
Relative size of right and left testes, *Thunnus alalunga* ($n = 106$).

Relative size of testes	Percent occurrence
Right larger than left	72
Right equal to left	2
Right smaller than left	23
No data	3

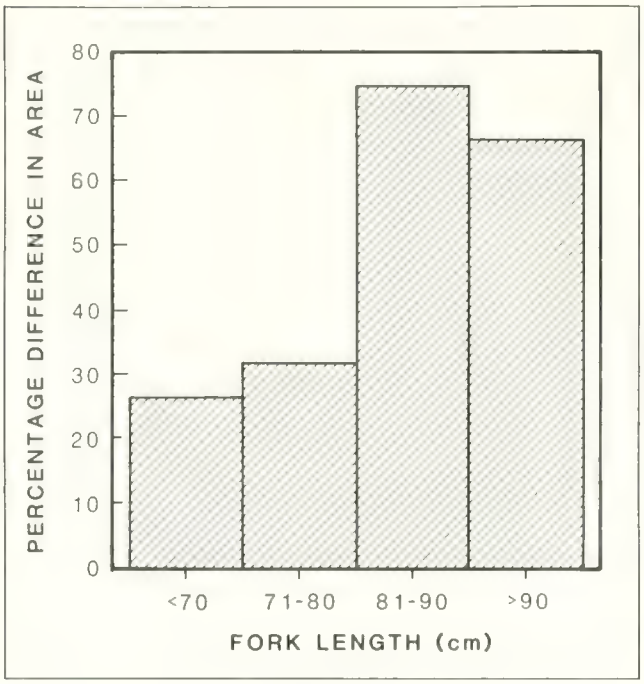

Figure 3
Percentage difference in cross-sectional area of the medial sections of right and left testes of South Pacific albacore, by fork-length.

right and left testes showed that the sizes of both gonads increase exponentially with increasing length of the fish, and that the area of the right testis does not increase at a faster rate than the left.

In summary, the right testis is predominately larger than the left; however, they both appear to increase in size at similar rates as the fish increases in length.

Histology of testes

The albacore testis has a lobular-type cellular arrangement, characteristic of most teleosts (Billard et al. 1982). We classified the germ cells into the following phases of development: spermatogonia, primary spermatocytes, secondary spermatocytes, spermatids, and spermatozoa.

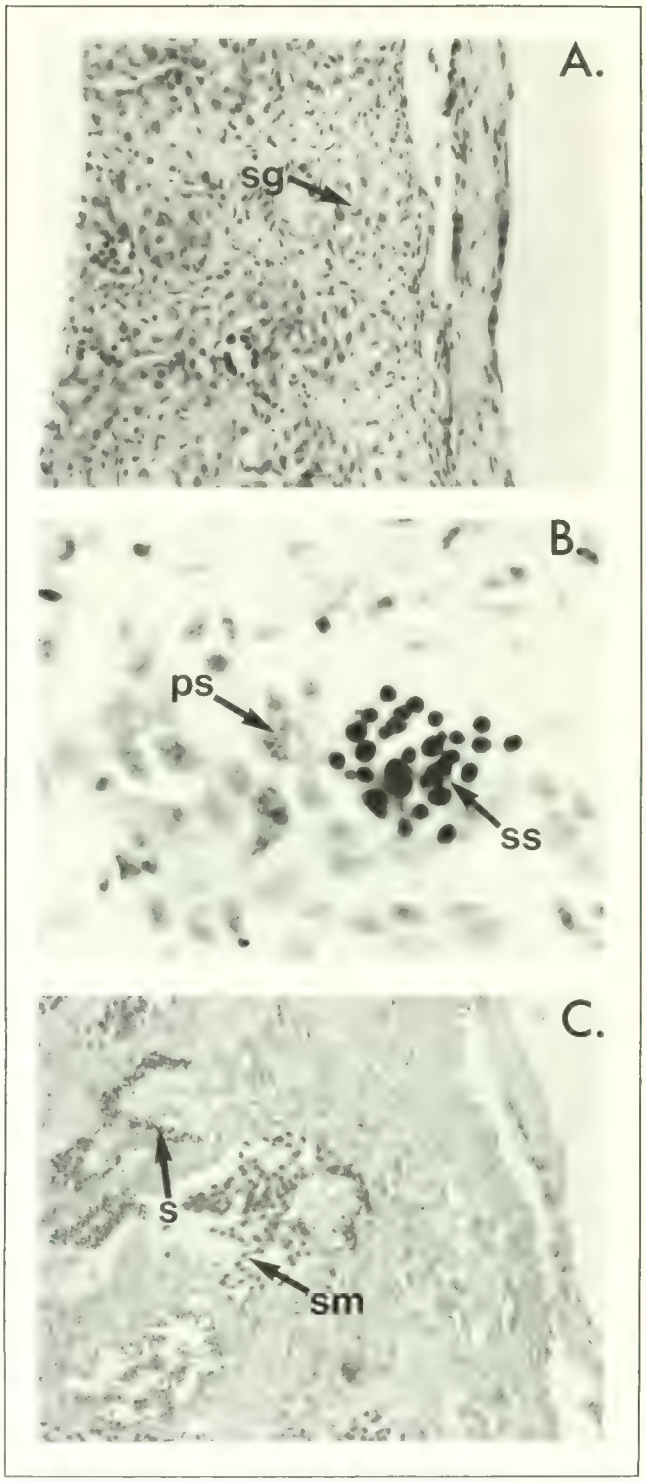

Figure 4
Spermatogenic cells observed in testes of South Pacific albacore. (A) Spermatogonia (sg) situated on lobule wall (×400); (B) primary spermatocyte (ps) cells and secondary spermatocyte (ss) cells (×600); (C) spermatids (sm) and spermatozoa (s) (×400).

Figure 5
Electron micrograph of South Pacific albacore spermatozoa (scale indicates 1 μm).

The primary spermatogonia are the largest cells with diameters of 12–16 μm. They have a prominent nucleolus, are basophilic, and are found in cysts with varying numbers of individual cells. The cysts are usually found singly near the periphery of the testis; a cyst situated on the lobule wall is shown in Figure 4A.

Primary spermatocytes are oval or spherical with diameters of 8–12 μm. They have no visible nuclear membrane and the chromatin material occupies most of the cell. Figure 4B shows examples of primary spermatocytes. Secondary spermatocytes are very small, spherical cells with diameters of 4–7 μm. Unlike primary spermatocytes, the chromatin is found in a clumped condition, similar to the spermatids. The cells occur in groups and are strongly basophilic. Figure 4B shows secondary spermatocytes.

Spermatids are strongly basophilic spherical cells with diameters of 2–4 μm. As they mature, they become smaller and the chromatin becomes uniformly condensed. Figure 4C shows that after detaching from the lobule wall, the spermatids remain in dense clusters.

The spermatozoa have a rounded nucleus and are morphologically subdivided into head, neck piece, short midpiece, and tail; as in other teleosts, there is no acrosome. They measure 1–2 μm in diameter, excluding the tail. An electron micrograph of an individual sperm is shown in Figure 5.

Table 3
Differences in meiotic activity between right and left testes, *Thunnus alalunga* ($n = 106$).

Meiotic activity	Percent occurrence
Left < right	10
Left = right	26
Left > right	61
No data	3

Meiotic activity

Relative abundances of sperm, spermatids, and spermatocytes were taken as a measure of meiotic activity. As previously discussed, the albacore testes were generally asymmetrical in size with the right testis more often larger than the left. However, we found that meiotic activity and sperm-duct development showed the opposite relationship. The left testis was meiotically more active than the right in 61% of males examined, the left and right testes had about equal activity in 26%, and the right was more active than the left in 10% (see Table 3).

Examination of data for each pair of testes showed a 60% occurrence of greater meiotic activity in the left testis relative to larger size of the right testis. Other combinations of meiotic activity and relative size of testes showed a 15% or less occurrence (see Fig. 6).

Relative abundance of sperm, spermatids, and spermatocytes

Absolute counts of the number of spermatogenic cells would be exceedingly difficult to make. Instead we estimated relative abundances of spermatocytes, spermatids, and sperm present using the categories *none*, *few*, *some*, and *many*. The results show that for all sizes of fish, the relative abundance of sperm was higher in the left testis than the right testis. For example, there were nearly 2 times more *many* and 2½ times fewer *none* categories of sperm observed for the left than the right testis. In both the left and right testes of fish in all sizes, relative abundance of sperm was highest in the caudal portion and decreased towards the rostral end (Figure 7).

The findings are similar for spermatids and spermatocytes, but the differences between testes are not as pronounced as those for sperm. For all sizes of fish, relative abundances of both spermatids and spermatocytes were higher in the left than the right testis. For the left testis, there were about 20% and 30% more *many* and 40% and 50% fewer *none*, categories observed for spermatids and spermatocytes, respectively,

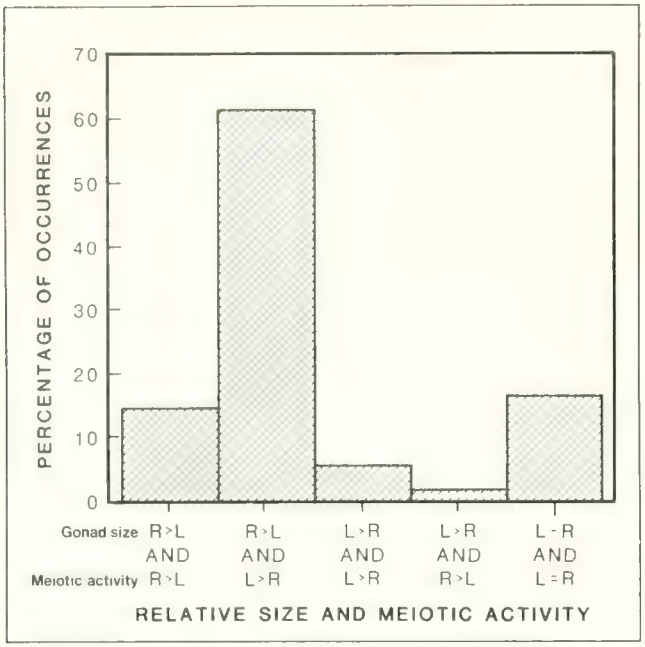

Figure 6

Percentage occurrence of relative level of meiotic activity and relative size of right (R) and left (L) gonads of South Pacific albacore. On the abscissa, upper expression refers to relative gonad size, and lower expression refers to relative level of meiotic activity.

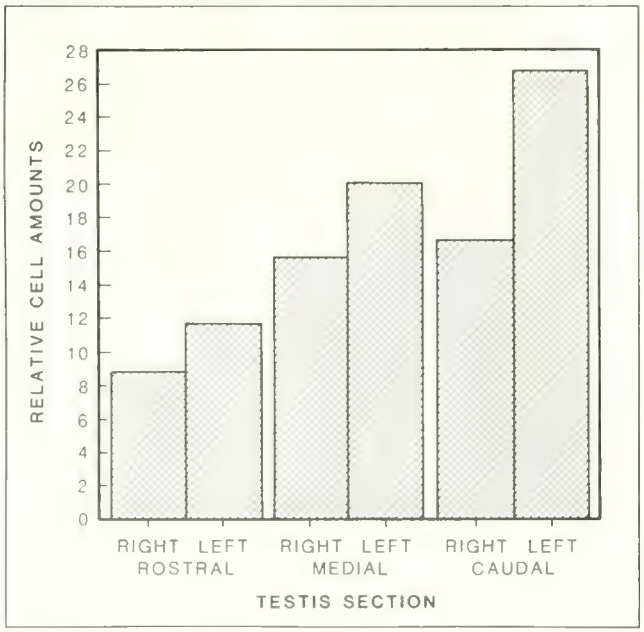

Figure 7

Relative abundance of sperm in rostral, medial, and caudal portions of the right and left testes of South Pacific albacore.

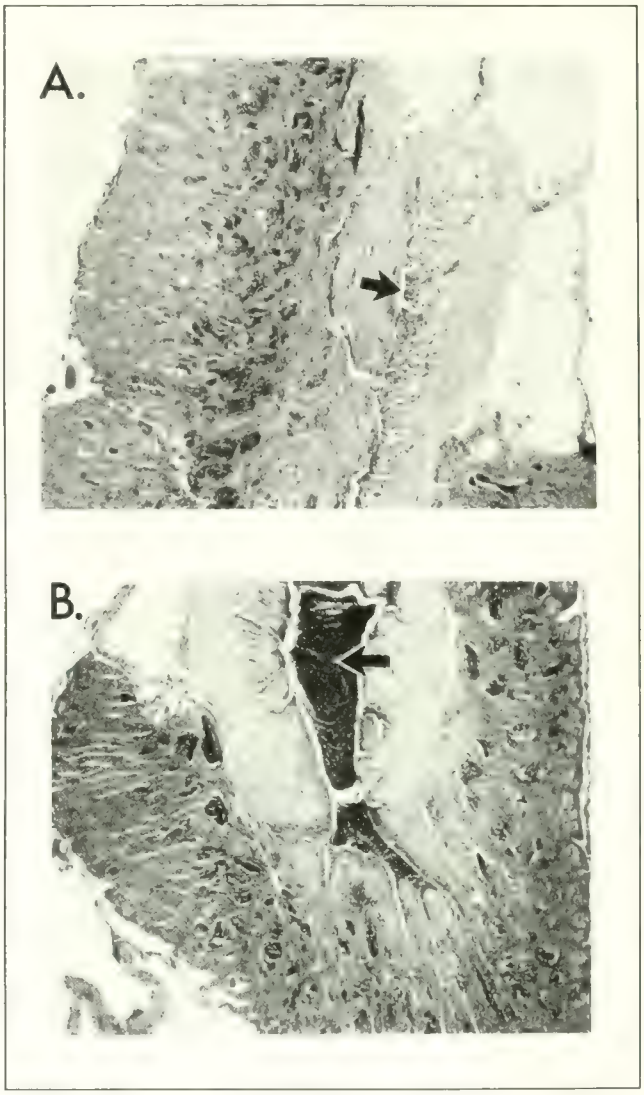

Figure 8

(A) Empty sperm duct of an immature South Pacific albacore; (B) sperm duct of a mature albacore filled with sperm, ×100.

than for the right testis. The relative abundance of each group of germ cells was highest in the caudal portion and decreased towards the rostral portion in both the left and right testes in all sizes of fish.

Sperm duct development

During testicular morphogenesis, teleost sperm ducts are formed by somatic cells derived from the somatic wall (Nagahama 1983). The main duct is present in immature albacore testes (Fig. 8A) in which no sperm are found. In mature albacore, we observed that the sperm duct is located near the center of the testis (Fig. 8B) and that a branching system of tubules radiates toward and end blindly at the testicular periphery. These obser-

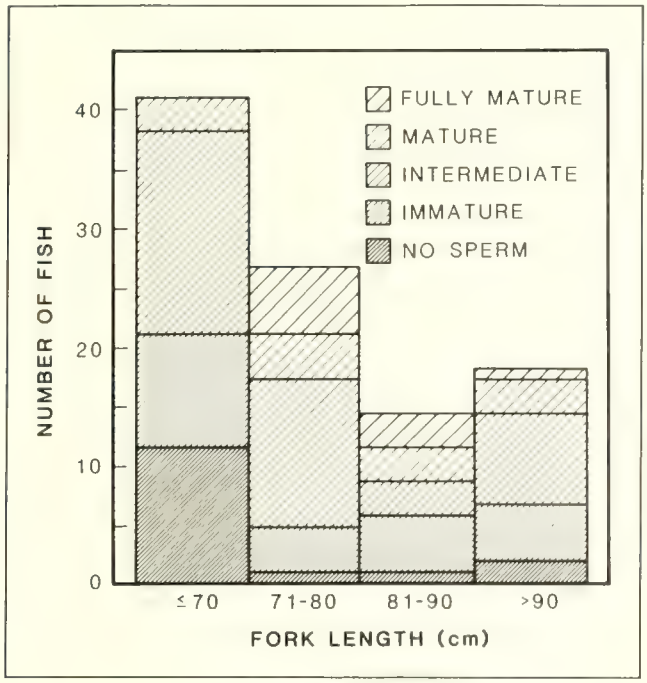

Figure 9
Comparison of sexual maturity levels of male South Pacific albacore by fork length.

Table 4
Percentage sexual maturity of fish by fork length.

Stage of sexual maturity	Fork length (cm)			
	<70	71–80	81–90	>90
No sperm present and immature	51	18	40	37
Intermediate	42	46	20	42
Mature and fully mature	7	36	40	21

vations differ from those reported for many other teleosts, where the main duct is located along the dorsal surface of the testis and may not be present in immature stages of the testis (Grier et al. 1980).

As the production of sperm increases, morphological changes occur in the main sperm duct. In the immature testis the main sperm duct is thin-walled and highly convoluted (Fig. 8A). In the mature testis the main duct, when filled with sperm, has much thicker walls and is less convoluted and more rounded (Fig. 8B). The production of sperm is also associated with increased vascularization of the testis, first in the caudal portion followed by the medial and rostral portions.

Ratios of observations characterizing immature and mature stages of sperm-duct development (thin:thick, convoluted:round, large:small) showed a higher proportion of mature sperm ducts in the left testis than the right. The results also reveal that sperm-duct development is greatest in the caudal, intermediate in the medial, and least in the rostral portions of both the right and left testes. As expected, there was an increasing trend in sperm-duct development with increasing fork length.

Sexual maturity

Fish were classified into five levels of sexual maturity based on relative abundance of sperm observed in the testes: (1) No sperm present in any portion of either testis; (2) immature, few sperm observed in one or more portions of either or both testes; (3) intermediate, few or some sperm in more than one portion of both testes, but not the sperm duct; (4) mature, many sperm observed in most portions of both testes and the sperm duct; and (5) fully mature, many sperm observed in all portions of both testes and the sperm duct.

Information on sexual maturity in relation to fork-length size categories is given in Figure 9 and Table 4. Slightly more than 50% of fish 50–70 cm FL were immature, including 28% (derived from Figure 9) with no sperm present in any portion of either testis. Over 40% were in the intermediate level and 7% were judged sexually mature, but none was fully mature. Fish in size groups larger than 70 cm FL had a lower proportion of immature individuals than did fish less than 70 cm, ranging from 18% to 40% (Table 4), including only 3–10% with no sperm present in any portion of either testis (derived from Figure 9). The proportion of fish in the intermediate level of maturity ranged between 20% and 46% for fish in size groups larger than 70 cm FL. The percentages of fish in the mature and fully mature categories were nearly the same for size groups 71–80 cm and 81–90 cm FL, 36% and 40%, respectively, but only 21% for the size group over 90 cm. The 71–80 cm FL size group had the highest proportion of fully sexually mature individuals, 23%, while only about 5% of fish larger than 90 cm were fully sexually mature (derived from Figure 9).

The lower proportion of mature and fully mature individuals in the size group larger than 90 cm FL appears to be related to geographic region and/or type of fishing gear. Figure 10 compares maturity levels between fish caught in the midocean region of the central South Pacific by surface trolling and those caught in coastal waters off New Zealand by subsurface longline. It is evident in Figure 10 that a higher proportion of immature and a lower proportion of mature and fully mature individuals were caught in coastal waters than in the midocean region, even though the longline-caught fish were much larger, averaging 92.3

cm FL, than troll-caught fish, averaging 69.2 cm. Figure 1 shows that virtually all of the fish in the size category greater than 90 cm were caught in coastal waters by subsurface longline.

Fat body

A lobulated mass of fat-like tissue was usually observed in the mesentery attached to testes and ovaries. In some cases it was extremely large and well developed, but quite rudimentary in others. It was generally white-to-creamy in color and always formed in segmental lobes. The extent of the fat body was usually coincident with that of the gonad, but sometimes it extended a variable distance anteriorly beyond the gonad. The mass of the fat body was generally correlated with size of the gonad. We observed that the right testis or ovary of the albacore, which is generally larger than the left, usually had a larger fat body (see Figure 2). In addition, we observed that the fat body was proportionately larger in immature fish that were meiotically inactive than in fish with gonads actively producing sperm.

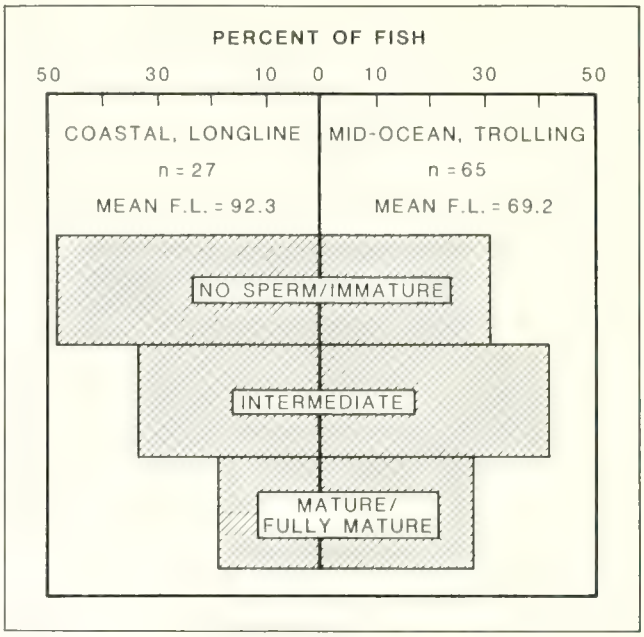

Figure 10
Comparison of sexual maturity levels of male albacore caught in coastal South Pacific waters by subsurface longline (left) with those caught in midocean South Pacific region by surface trolling (right).

Discussion

According to literature pertaining to the general structure and function of teleost gonads, the development of gonads is usually similar on both sides of the fish. However, asymmetry in gonad size has been observed sometimes in some species, usually at or near the time of breeding (Turner 1919, Robertson 1957, Sanwal and Khana 1972, Dalela et al. 1977).

Asymmetry in gonad size appears to be common for albacore, at least in prespawning stages. We observed asymmetry in 95% of fish examined, with the right gonad larger than the left in 72% of the cases. The disparity in size increased with increasing fork length. The right testis averaged about 30% larger than the left in fish less than 80 cm and averaged more than 70% larger in fish greater than 80 cm. We do not have data collected during active spawning to ascertain if this relationship exists at that stage.

Otsu and Uchida (1959) reported that the right ovary was usually slightly larger than the left in albacore specimens from the central North Pacific, but they did not quantify the difference. Ueyanagi (1955) noted that the right and left ovaries from a mature female albacore caught in the Indian Ocean differed in weight by 100 grams. However, he did not indicate weights or relative size of the ovaries. Partlo (1955) conducted histological studies on 44 albacore from the eastern North Pacific, but did not publish data on gonad size or mention asymmetry. The gonads of other tunas are more or less symmetrical in size and usually have no conspicuous fat body (Kurt Schaefer, Inter-Am. Trop. Tuna Comm., P.O. Box 271, La Jolla, CA 92038, pers. comm., 1 May 1989).

The finding that meiotic activity is higher in the smaller of a pair of testes is puzzling, and we have no ready explanation for it. It may be that this relationship holds true only for prespawning individuals and possibly during other periods when albacore are not spawning. We are unable to determine whether this condition continues through the spawning cycle because our samples were collected over an insufficient period and not in the primary geographic region where South Pacific albacore are believed to spawn (Otsu and Hansen 1961). A remote possibility is that the smaller testis is kept in an advanced reproductive state for "opportunistic" spawning and that the larger testis matures only when the fish is in the more prevalent location of spawning. If this is so, the species could presumably extend its reproductive potential with relatively low expenditures of energy. It is also possible that sperm are not shed by precocious fish, but are reabsorbed. Progressive reabsorption of sperm by sertoli cells has been observed in rainbow trout (van den Hurk et al. 1978).

Our results show that some males less than 70 cm may be sexually mature and that the proportion of sexually mature individuals increases with increasing fork length, up to 90 cm. There is a decrease in the percent-

age of sexually mature males in the size category above 90 cm FL which may be related to the method of capture and/or the type of habitat where collected. All fish larger than 90 cm, except one, were caught during subsurface longline fishing operations within about 75 miles of the coast of the New Zealand north island, whereas nearly all other fish were caught by surface trolling in midocean waters. Oceanographic observations made concurrently with albacore troll-fishing operations indicate that albacore in the midocean region of the South Pacific are associated with Subtropical Convergence Waters (Laurs 1986, Laurs et al. 1987).

Female albacore have been reported to attain sexual maturity and first spawn at about 90 cm FL (Ueyanagi 1955, Otsu and Uchida 1959); however, size at maturity for males has not been well established. Otsu and Hansen (1961) found that some male albacore are probably mature when they attain a length of about 90 cm FL. Based on the general appearance of testes and oozing of milt, Ueyanagi (1957) postulated the smallest mature male to be 97 cm FL in a sample of albacore collected in the western North Pacific. Brock (1943) reported that "Milt could be squeezed from the testes of some of the more mature males, but no females were found in which eggs could be discerned by the unaided eye...." Brock (1943) examined fish caught off the Oregon coast that ranged in fork length between 53 and 90 cm, but did not specify the size of fish that contained milt.

Partlo (1955), in the only published histological study that includes albacore testes as well as ovaries, concluded that both males and females in his age groups V and VI were in a condition approaching spawning. He calculated that the mean fork length for males and females in age-group V is approximately 70 cm, and for age-group VI is about 85 cm for males and 79 cm for females. He also reported observing small numbers of fully mature sperm restricted to tubules of the posterior portion of testes in age-group IV, which he reported as having a mean fork length of 62 cm. Partlo (1955) examined a total of 44 testes and ovaries, but unfortunately did not specify the sex or number of individuals in each age group.

Godsil and Byers (1944) reported that the fat body was present in albacore collected throughout the North Pacific, except in three specimens from the area around the Hawaiian Islands, with its greatest development always on the right side of the fish. However, they made no mention of asymmetry in gonad size.

There appears to be a functional relationship between meiotic activity and the amount of fat in the mesentery. We presume the fat body provides an energy source for spermatogenesis, although we have no information from the present study on the timing of sperm release from the albacore testis. Godsil and Byers (1944) also speculated that the fat body acts as an energy reserve for female albacore that is expended during the spawning season. They based their supposition on the absence of the fat body in three recently spawned albacore from the Hawaiian Islands. Schaefer (1987) noted that spawning in the black skipjack, *Euthynnus lineatus*, is probably regulated by energy available in fat storage. When the fat stores fall below a minimum level, ovarian atresia probably occurs over a short period of time.

Conclusions

We provide quantitative evidence that a substantial portion of male albacore caught in midocean areas of the South Pacific Subtropical Convergence Zone about lat. 35°–40°S, may be sexually mature when they attain a fork length of 71–80 cm. Also, the proportion of mature fish increases with increasing length. A lower proportion of males caught by subsurface longline fishing in coastal waters off New Zealand showed development in sexual maturity, although not as accelerated as males caught by surface trolling in the midocean region. Female fish 55–95 cm FL caught in both regions showed few signs of sexual maturation. South Pacific albacore are believed to spawn generally in the region of the Southern Tropical Convergence waters about lat. 20°–10°S (Knox 1970). This region is about 1000–1500 miles north of the Subtropical Convergence Zone where the albacore investigated in this study were caught.

The adaptive significance of sexual maturity in male albacore at times, locations, and ages when females are not in spawning condition is not clear. Sampling of both males and females over the entire spawning cycle and in locations where albacore are believed to spawn will be required to understand the reproductive biology of the South Pacific albacore population.

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Age Estimation and Composition of Pelagic Armorhead *Pseudopentaceros wheeleri* from the Hancock Seamounts

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The pelagic armorhead *Pseudopentaceros wheeleri* is widely distributed in the North Pacific, but rarely collected until fishermen from the Soviet Union discovered large concentrations on the central North Pacific seamounts in the late 1960s (Sakiura 1972). The Soviet Union started a trawl fishery at the southern Emperor–northern Hawaiian Ridge (SE–NHR) seamounts (29°N, 179°E to 35°N, 171°E) in 1967, and the Japanese entered the fishery in 1969 (Sasaki 1986). Since then, intensive fishing occurred at the Northwest and Southeast Hancock Seamounts, the southeast limit of the pelagic armorhead seamounts. During the 1970s, the pelagic armorhead catch rate by Japanese fishing vessels at the Hancock Seamounts declined dramatically (Uchida and Tagami 1984). Commercial fishing at the Hancock Seamounts ceased in 1984, and finally, a 6-year fishing moratorium went into effect in August 1986 (NMFS 1986).

Pelagic armorhead have an unusual life history. At SE–NHR seamounts, adults spawn during December–March, as indicated by ovarian studies (Sasaki 1974, Bilim et al. 1978) and the occurrence of larvae and young juveniles in February and March (Borets 1980). As juveniles, they apparently are pelagic and occur to the north and northeast of the seamounts as far as the Alaskan gyre before returning to the seamounts (Fujii 1986, Boehlert and Sasaki 1988). At the SE–NHR seamounts, most of the pelagic armorhead caught in the fishery are 26–33 cm fork length (FL), although 15–40 cm FL specimens occur (Humphreys and Tagami 1986). Larger specimens (>40 cm FL), but none 26–33 cm FL, have been caught on the northern Hawaiian Ridge, from Kure Atoll to French Frigate Shoals (Tagami and Humphreys, in prep.).

Pelagic armorhead at the seamounts exhibit three morphological types: fat, intermediate, and lean (Humphreys et al. 1984, 1989; Humphreys and Tagami 1986). During their pelagic phase and when they recruit to seamounts, they are "fat" and their gonads are in an early stage of development. When gonads begin developing and spawning occurs, they transform from an "intermediate" to a "lean" stage. It has not been determined whether the lean fish recover to spawn again.

In this study, we determined which hard part is the most suitable for estimating armorhead age and determined the temporal meaning of perceived daily growth increments and apparent annual check marks on the sagitta, the preferred hard part. Chikuni (1970) and Vasil'kov and Borets (1975) used annuli on scales to estimate age, but their estimates did not agree. Furthermore, neither study used validation procedures, nor did they document the area of collection. The criteria we developed were used to estimate the age composition of pelagic armorhead captured on Southeast Hancock Seamount.

Methods and materials

Specimen collection

Pelagic armorhead were obtained at the Hancock Seamounts in 1976–85 from the Japanese trawler *Kitakami Maru*, and by bottom trawl and handline from the NOAA ship *Townsend Cromwell*. Random samples were obtained by pooling specimens from bucket scoops (range 2–100 kg/haul) on the *Kitakami Maru*, during 1 August–15 October 1981, and from a single haul on the *Townsend Cromwell* on 24 July 1984. Fish were measured for FL to the nearest millimeter and sexed by gonadal examination. Fish were classified, on the basis of color and body depth, to one of three body types: fat, intermediate, or lean (Humphreys et al. 1984). We also included a few very large specimens caught by handline on the northern Hawaiian Ridge seamounts between Kure Atoll and French Frigate Shoals and postlarvae caught in a surface tow with a Tucker trawl at Southeast Hancock Seamount, 23–24 February 1985. All postlarval specimens were preserved and stored in 70% ethanol.

Hard-part selection and check-mark counts

To determine which hard part was most suitable for estimating age, 13 structures (Table 1) were dissected from 5 specimens collected at the Hancock Seamounts. The structures were prepared for examination following modified procedures of Six and Horton (1977). The hypural

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Table 1

Comparison of check marks on various hard parts of five *Pseudopentaceros wheeleri* from the Hancock Seamounts.

	No. check marks by fish identification number				
Hard part	343	350	338	385	383
Sagitta	3	3	–	3	2
Centrum (vertebra)	3	3	3	3	2
Dorsal spine	3	3	3	3	2
Dorsal ray	0	0	0	0	0
Anal spine	3	0	3	3	2
Anal ray	0	0	0	0	0
Pelvic spine	0	0	3	3	0
Pelvic ray	0	0	0	0	0
Pectoral spine	0	0	0	0	0
Pectoral ray	0	0	0	0	0
Hypural	3	3	3	3	2
Maxillary	0	0	3	3	2
Scales	0	–	–	–	0

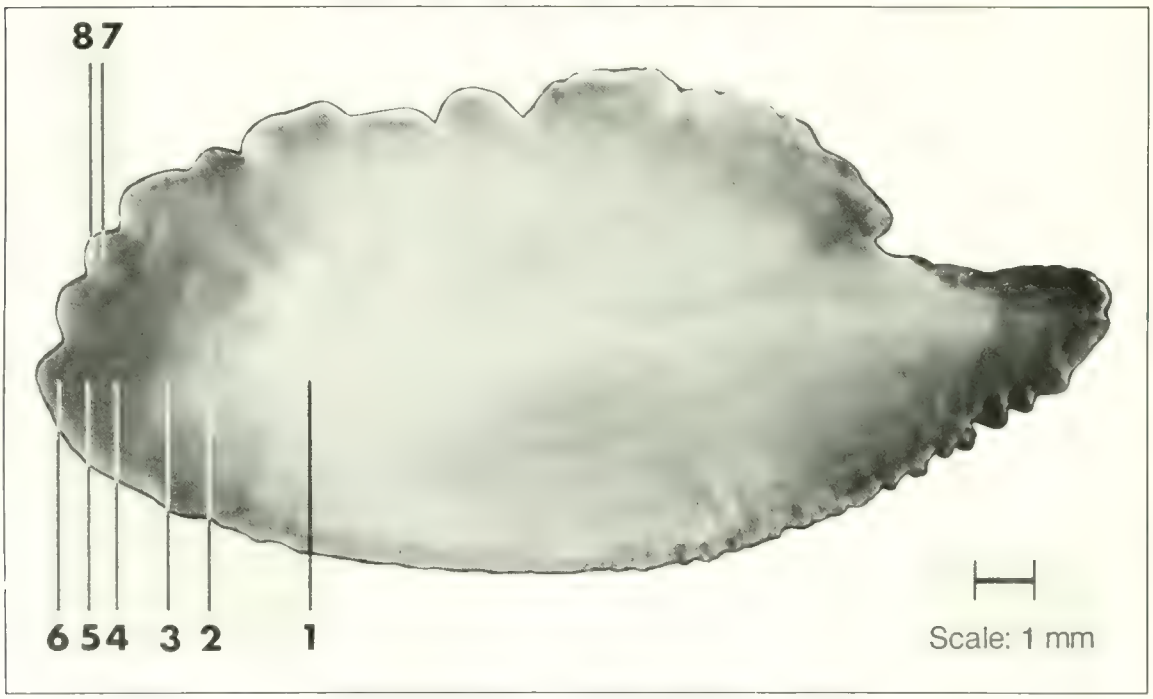

Figure 1

Sagitta of *Pseudopentaceros wheeleri* with annuli marked and numbered.

plate, maxillary, and vertebrae were cleaned of tissue and dried. Spines and rays of the dorsal, pelvic, pectoral, and anal fins were cleaned of tissue, embedded in resin, cross-sectioned in a continuous series from the base, and examined under a compound microscope. Both surfaces of a section were examined. Tissues were also examined under a dissecting microscope with reflected and transmitted light.

Sagittae were sanded lightly on the surfaces with no. 400 grit carborundum sandpaper, then, with a dissecting microscope, were examined whole against a black background while submerged in water. Check marks appeared as pairs of bright (opaque) and dark (translucent) concentric bands under reflected light (Fig. 1).

Scales were taken from nine different areas of the body. Three sites were along the lateral line: below the

first dorsal spine, midway along the lateral line, and below the posterior end of the dorsal fin. Three sites were midway between the lateral line sites and the dorsal fin, and three were midway between the lateral line sites and the ventral border. Scales were taken from 20 fish of three different body types and from 13 fish, caught in February 1985, with three check marks on their sagittae. After being cleaned, scales were mounted in Euparal under a cover glass on a glass slide or flattened between two glass slides after being air dried.

Selection of the hard part for ageing was based on the consistency of perceived annual check mark counts and ease of preparation (Table 1). Only the sagittae, vertebral centrum, hypural plate, and dorsal and anal fin spines showed check marks. Counts of check marks from each part were identical (Table 1), indicating these structures could be used for estimating age if their check marks could be verified as annuli. The number of check marks on vertebral centrum, hypural plate, and maxillary was reduced by half upon drying. Soft rays of dorsal, pelvic, pectoral, and anal fins showed no marks that could be interpreted as check marks. Scales were without check marks, and their circuli appeared evenly spaced. Of all the structures compared, the sagitta was considered the best structure for estimating the age of pelagic armorhead.

Counts of daily growth increments

Sagittae removed at sea were stored in fresh water in vials and refrigerated; those not extracted at sea were frozen within the head and later removed in the laboratory. Sagittae were sanded lightly on both sides with no. 400 carborundum sandpaper until translucent and etched in a very dilute solution of HCl for 3–5 minutes. The acid was diluted until only 1–2 bubbles per second were formed in reaction to the calcium carbonate of the sagitta. This process was repeated until the increments became visible from the core to the tip of the postrostrum. The sagittae of postlarval specimens were teased from the skull, cleaned, and mounted in Euparal without further processing. To support the coverslip, each sagitta was mounted on a microscope slide in Euparal by using short segments of monofilament line slightly greater in diameter than the thickness of the otolith. Sagittae were examined under a compound microscope at 300× magnification.

Increment counts often took a circuitous route between the core and the tip of the postrostrum; the mean of 10 counts was used as the age estimate. Increment counts were routine for sagittae with two check marks but were more difficult for those with three check marks. Increment width in translucent zones decreased with increasing number of check marks (8.3 μm during year 1, 1.7 μm during year 2, and 1.5 μm during year 3), and incremental pattern was more variable after year 2.

Age estimation

Check marks could not be validated as annuli by conventional means (Beamish and McFarlane 1983). Mean increment counts were used to estimate the hatching time, assuming the first increment formed at or soon after hatching. This technique, though low in accuracy, may suffice when direct validation is unattainable (Gjøsaeter et al. 1984). To verify check marks as annuli, mean counts of growth increments for fish caught in February were then compared with counts of check marks, which were multiplied by 365.

Age composition of catches of pelagic armorhead at Southeast Hancock Seamount was based on check-mark counts (i.e., perceived annuli). Mean FLs between age-sex groups were compared using the Mann-Whitney paired test, since unequal variances occurred in one sample. To increase sample size of age-sex groups from the *Kitakami Maru* catch, randomly sampled specimens from Northwest and Southeast Hancock Seamounts were combined.

Results and discussion

Increment counts from demersal and oceanic adults and juvenile pelagic armorhead suggested that increments were deposited daily (Tables 2 and 3). A total of 88% of the estimated hatching dates of adults occurred within the spawning period, and the other three hatching dates were reasonably close to the spawning period.

Check marks appeared to be valid annuli based on number of daily growth increments for fish caught in February (Table 2). Sagittae with two check marks had approximately 730 increments (range 728–773, $N = 5$), and those with three check marks had about 1095 increments (range 1037–1128, $N = 4$). Check marks were also verified as annuli by a second but less precise method (Pannella 1971). Partial counts of 365 apparent daily growth increments appeared to coincide closely with the first pair of opaque and translucent zones of sagittae of age-1 and -2 fish. Partial counts of about 730 apparent daily growth increments corresponded with the outer margin of the second translucent zone on sagittae of age-2 fish.

Fish caught in summer appeared to have completed check marks on their sagittae. Sagittae from fish caught in July with two check marks had increment

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Table 2

Age estimates of pelagic armorhead *Pseudopentaceros wheeleri* by counting apparent daily growth increments (GI) on sagittae.

Date captured	Fork length (mm)	Sex	Mean GI count	SD	Estimated hatching date	No. check marks	Body type
29 Oct. 1976	277[a]	M	623	25.63	8 Feb. 1975	2	—
18 June 1983	340	F	902	13.04	29 Dec. 1980	3	Fat
12 July 1984	300	F	576	24.03	13 Dec. 1982	2	Lean
12 July 1984	322	F	621	21.67	30 Oct. 1982	2	Intermediate
13 July 1984	305	M	549	43.83	10 Jan. 1983	2	Intermediate
13 July 1984	308	F	937	58.00	18 Dec. 1981	3	Lean
24 July 1984	309	M	907	94.29	28 Jan. 1982	3	Fat
24 July 1984	310	M	544	37.28	26 Jan. 1983	2	Fat
24 July 1984	322	M	923	92.46	13 Jan. 1982	3	Fat
24 July 1984	329	F	605	37.94	26 Nov. 1982	2	Fat
25 July 1984	307	F	586	37.16	16 Dec. 1983	2	Intermediate
25 July 1984	319	F	914	39.99	22 Jan. 1982	3	Intermediate
29 July 1984	303	M	853	51.39	28 Mar. 1982	3	Intermediate
16 Feb. 1985	282	M	728	46.10	18 Feb. 1983	2	Lean
16 Feb. 1985	290	M	1037	26.80	15 Apr. 1982	3	Lean
16 Feb. 1985	293	M	762	50.96	15 Jan. 1983	2	Fat
16 Feb. 1985	304	F	758	40.53	19 Jan. 1983	2	Lean
16 Feb. 1985	311	F	761	45.73	16 Jan. 1983	2	Lean
16 Feb. 1985	317	M	773	27.29	4 Jan. 1983	2	Lean
16 Feb. 1985	319	F	1128	79.66	14 Jan. 1982	3	Lean
16 Feb. 1985	320	F	1101	84.65	10 Feb. 1982	3	Lean
23 Feb. 1985	355	F	1065	51.32	25 Mar. 1982	3	Fat
25 July 1984	322[b]	M	951	69.04	16 Dec. 1981	3	Fat
25 July 1984	305[c]	—[d]	599	35.83	3 Dec. 1982	2	Fat
25 July 1984	310[e]	F	580	52.73	22 Dec. 1982	2	Fat

[a] Estimated from standard length.
[b] *Oshoro Maru*, lat. 45°26′N, long. 154°58′W.
[c] *Oshoro Maru*, lat. 45°26′N, long. 155°00′W.
[d] Gonad undeveloped.
[e] *Oshoro Maru*, lat. 45°26′N, long. 155°00′W.

Table 3

Age estimates of postlarval *Pseudopentaceros wheeleri*, determined by counts of apparent daily growth increments (GI) on sagittae.

Fork length (mm)	Capture date	Mean GI count	SD	Estimated hatching date
12.1	24 Feb. 1985	36.5	1.72	19 Jan. 1985
12.1	24 Feb. 1985	34.7	1.89	20 Jan. 1985
13.4	24 Feb. 1985	39.6	2.41	15 Jan. 1985
13.6	23 Feb. 1985	42.1	2.02	12 Jan. 1985
13.6	24 Feb. 1985	41.9	2.64	12 Jan. 1985
15.9	23 Feb. 1985	41.9	2.28	12 Jan. 1985
15.9	23 Feb. 1985	48.0	5.16	6 Jan. 1985
18.2	23 Feb. 1985	57.7	5.93	27 Dec. 1984

counts (544–621) roughly equivalent to 1.5 years, and those with three check marks had increment counts (853–937) roughly equivalent to 2.5 years (Table 2). In July, sagittae of age-1 and -2 fish appeared to have two and three translucent zones, respectively. The outer translucent zone probably was due to thinness at the edge of the sagittae. Another possibility is that the opaque zone formed over a short period (<2 months) and formed internally in the translucent zone so that the outer edge was opaque for only a brief period. This has also been observed for *Ammodytes tobianus* (Reay 1972). Regardless, the result would be an overestimation of age for part of the year if fish were sampled prior to the spawning season.

Table 4

Mean fork lengths (FL) of pelagic armorhead *Pseudopentaceros wheeleri* age groups at the Southeast Hancock Seamount.

		Male FL (mm)				Female FL (mm)			
Sample date	Age	Range	Mean	SD	*N*	Range	Mean	SD	*N*
Aug.–Oct. 1981	1.5	267–320	294	14.07	37	285–325	307	9.54	68
	2.5	304–304	304		2	283–329	310	14.08	8
July 1984	1.5	247–330	301	15.57	37	295–331	308	8.22	39
	2.5	285–326	307	13.96	13	290–342	315	10.89	27

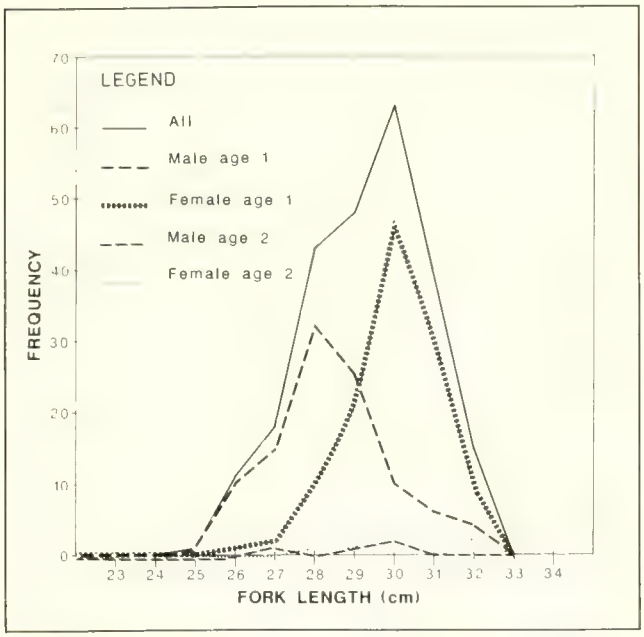

Figure 2

Length-frequency distribution of *Pseudopentaceros wheeleri* sampled at the Hancock Seamounts, 1 August–15 October 1981.

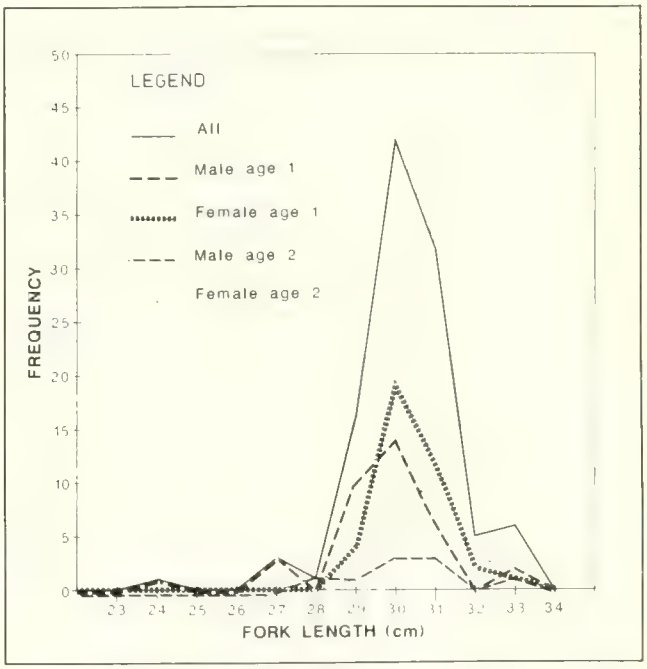

Figure 3

Length-frequency distribution of *Pseudopentaceros wheeleri* sampled at the Southeast Hancock Seamount, 24 July 1984.

We could not determine when the opaque zone formed because specimens were not obtainable throughout the year and the edge always appeared translucent.

Pelagic armorhead from the summer trawl fishery at the Southeast Hancock Seamount consisted of fish approximately ages 1.5 and 2.5, and yearlings were dominant in both 1981 (96%) and 1984 (66%) (Table 4). Yearling females appeared to be larger than males in both 1981 and 1984 samples (Figs. 2 and 3; Table 4). Differences between male and female mean lengths were significant in 1981 ($P<0.001$) and in 1984 ($P=0.025$), but difference in mean lengths for year-2 females and males in 1984 was not significant ($P=0.107$). The latter could have been due to small sample size; hence, larger samples should be examined before requiring separate growth curves for males and females. Our samples were not perfectly suited for group comparison because sex and age were unknown when the random samples were taken. Thus, unequal group size and unequal variances occurred. Due to our small sample size, slight skewness and kurtosis were encountered in comparing central tendencies of some age-sex groups. However, only the unequal variance between groups was serious enough to have affected the analyses.

Pelagic armorhead may attain sexual maturity before they reach the seamount. We base this on the age-length relationships of the three oceanic specimens (Table 2). After pelagic armorhead settle on the seamount, it appears that little growth occurs. Length-frequency distribution reported by other investigators (Sasaki 1986, Wetherall and Yong 1986) tends to confirm this observation. The lack of older (>age 3) individuals on the seamounts suggests that pelagic armorhead may spawn only one or two seasons and then die. Indeed, the presence of emaciated individuals suggests

some postspawning mortality (Humphreys et al. 1984, Humphreys and Tagami 1986). Conversely, the existence of larger and older specimens in the northwestern Hawaiian Islands would suggest that longer life is possible and different life histories occur in different environments. Of the sagittae from large pelagic armorhead examined for comparison purposes, fish 43–48 cm FL ($N = 3$) had four check marks, fish 48–54 cm FL ($N = 2$) had five check marks, and the largest fish, 54.7 cm FL, had eight-plus check marks (Fig. 1). Although the relationship of these large pelagic armorhead to those on the seamounts is unknown, it is plausible that during the pelagic stage juveniles were displaced to the east, entered the subtropical gyre, and grew larger while spending 1–3 years longer in the open ocean before settling in the northern Hawaiian Ridge seamounts, southeast of the SE-NHR seamounts (Boehlert and Sasaki 1988).

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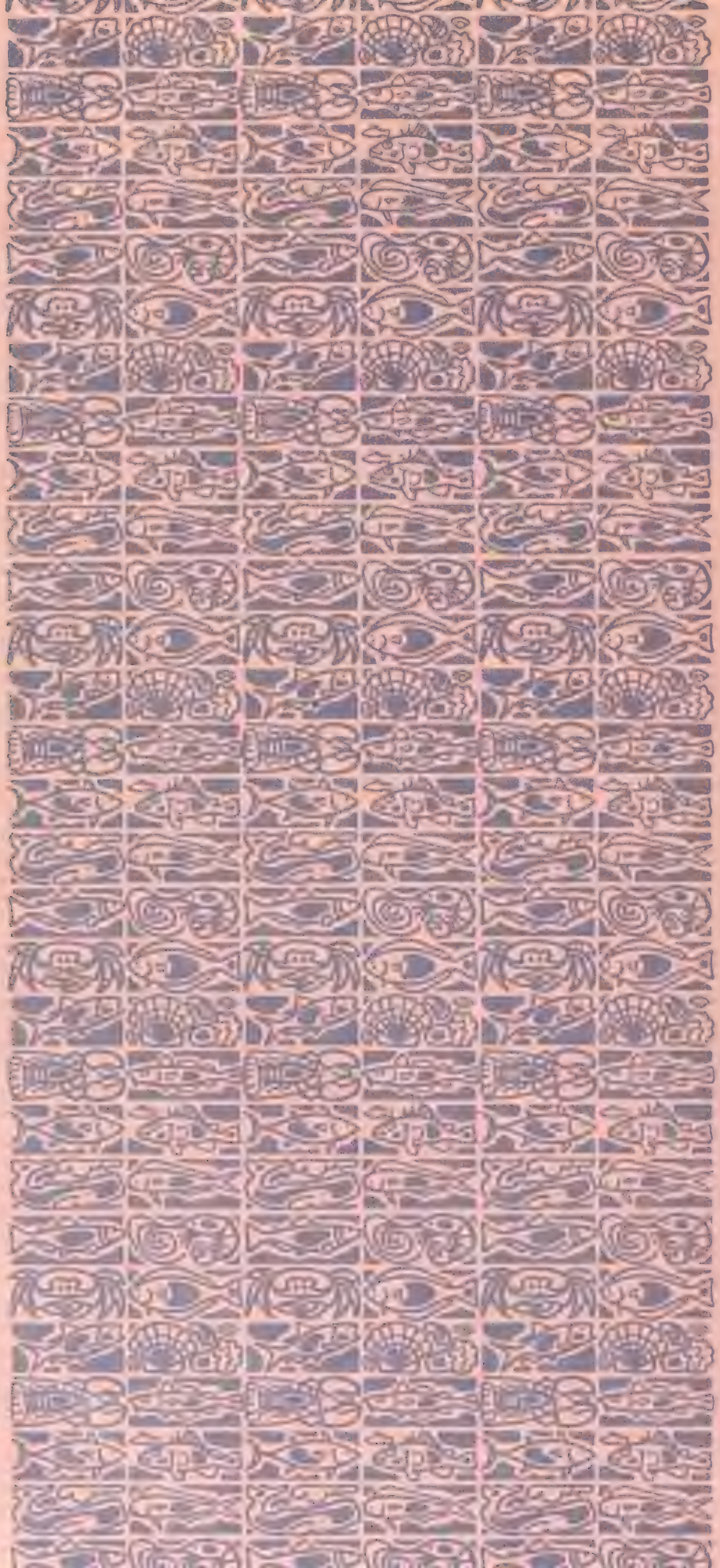

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Abstract.– Seasonal habitat use of young-of-the-year, subadult, and adult rockfishes (*Sebastes caurinus*, *S. maliger*, and *S. auriculatus*) were compared for four habitat types: high-relief rocky reefs, low-relief rocky reefs, high-relief artificial reefs, and sand/eelgrass. Diving surveys conducted December 1986 through October 1988 on two representative sites of each habitat type revealed significant seasonal changes in rockfish densities and habitat use. Young-of-the-year (YOY) recruitment varied between the two survey years: YOY were observed on all habitat types in the summer and fall of 1987, whereas they were observed at only one site (artificial reef) in a similar time period of 1988. High-relief rocky reefs had the most consistent densities of the three rockfish species, mostly fish >200 mm TL. Adult and YOY copper, quillback, and brown rockfishes were observed on the low-relief rocky reefs primarily in the summer months coincident with summer algal growth; when the kelp died back in the fall, most rockfishes left these reefs. The highest densities of rockfishes, primarily 80–200 mm quillback rockfish (up to 420/90-m^3 transect) and large copper rockfish (up to 56.3/transect), were observed on the artificial reefs. Here, also, density fluctuations were dramatic; copper rockfish densities peaked in fall and winter and declined (to 0/transect) during the summer, and quillback rockfish densities also seasonally fluctuated. Sand/eelgrass areas were the least-utilized habitat type; only during July and August were young-of-the-year and low densities of adult copper and brown rockfishes observed on one sand/eelgrass site. Although all four habitats were used, natural reefs may represent source habitats that are used by and maintain rockfishes on less productive sink (artificial reef) habitats. Thus, the recent use of artificial reefs as mitigation for the loss of natural reefs could have negative impacts on rockfish populations.

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A Comparative Study of Habitat Use by Young-of-the-year, Subadult, and Adult Rockfishes on Four Habitat Types in Central Puget Sound*

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Rockfishes are a successful group of marine fishes represented by about 100 species (Barsukov 1981), which occupy a variety of habitats ranging from the intertidal to the edge of the continental shelf (Lea 1983). This speciose and interesting group displays extremes in habitat use and movement patterns: Some species live deep (500 m) over sandy bottoms, some make long-distance movements (to 550 km), whereas others are perennially sedentary on shallow (<10 m) rocky reefs (Larson 1980, Love 1980, Culver 1987). One group of rockfishes is solitary and demersal and inhabits shallow reefs (Ebeling et al. 1980a); in Puget Sound this group of rockfishes is represented by copper *Sebastes caurinus*, quillback *S. maliger*, and brown *S. auriculatus*.

Copper, quillback, and brown rockfishes are common shallow-water benthic species found along the Pacific coast of North America (Hart 1973). They are morphologically similar to one another but differ in coloration. The three species have overlapping geographic ranges; copper and brown rockfishes are found from Baja California to Alaska, whereas quillback are found from central California to Alaska (Hart 1973). All three species occur in Puget Sound, Washington, and comprise approximately 25% of the recreational bottomfish catch in central Puget Sound (Palsson 1988). These species inhabit a variety of habitat types although highest densities are reported on artificial reefs, natural rocky reefs, and rock piles in water less than 30 m (Moulton 1977, Buckley and Hueckel 1985). Usually these species are found directly on the bottom closely associated with rock, artificial substrate, or vegetation (Patten 1973, Moulton 1977). Although copper and quillback rockfishes are common throughout Puget Sound, the San Juan Islands, and Strait of Juan de Fuca, brown rockfish are more limited in distribution and are found only within central and south Puget Sound (Moulton 1977).

Rockfishes are viviparous (Boehlert and Yoklavich 1984), undergoing internal fertilization and subsequently releasing pelagic larvae. Little is known regarding the length of time that young rockfishes are pelagic before they recruit to adult or transitional habitat. Parturition reportedly occurs April through June for the three species in Puget Sound (DeLacy et al. 1964, Washington et al. 1979, Dygert 1986). An influx of postlarval or young-of-the-year (YOY) rockfishes into isolated areas in Puget Sound has been observed (Patten 1973, Gowan 1983); assessment of habitat

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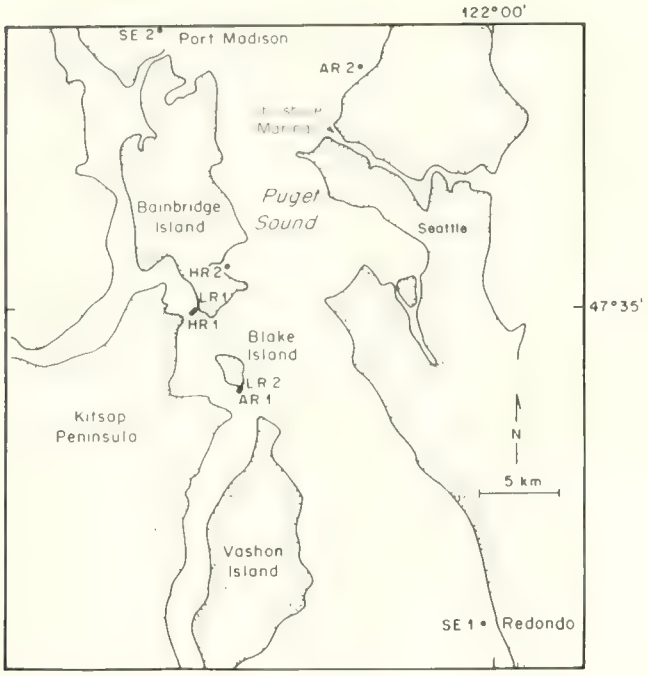

Figure 1
Map of study sites within central Puget Sound. HR1 Orchard Rocks, HR2 Blakely Point, LR1 Bainbridge Island, LR2 Blake Island, AR1 Blake Island, AR2 Boeing Creek, SE1 Redondo, SE2 Port Madison.

features required by recruits and different habitats utilized has been only qualitatively described. It is likely that habitat requirements of juveniles and adults differ, as juveniles may require shelter from predation and associate more closely with structural algal cover (Hobson 1972, Carr 1989). Ebeling and Laur (1985) experimentally demonstrated that young surfperches sought and were restricted to microhabitats that offered protection from predation. Carr (1983) suggested that kelp may provide a refuge from predation for YOY rockfishes including three species found offshore as adults (*Sebastes paucispinus*, *S. pinniger*, and *S. miniatus*), that recruit to kelp beds in central California. Because rockfish produce pelagically dispersed larvae and juveniles, local adult density is probably a poor predictor of local recruitment and future adult density. Rather, the limited availability of habitat with which young-of-the-year and juvenile associate may be the critical determinant of local recruitment. Determining the habitat requirements of young rockfishes can be crucial to our understanding of local rockfish dynamics. If algae, seagrasses, or other habitats provide YOY rockfishes essential shelter from predation and increased access to food, then recruitment could be suppressed by eliminating such shelter or enhanced by adding more shelter. Habitat affinities and requirements are an unknown for YOY and juvenile rockfishes in Puget Sound.

Copper, quillback, and brown rockfishes inhabit a variety of habitats, yet the relative importance of each habitat and seasonal uses are unknown. Additionally, differences in habitat use by different life-history stages are poorly understood. For example, do young rockfishes settle on reefs and remain there for life, or do the different age groups (young-of-the-year, subadult, and adult) later move to separate or different habitats? Understanding how and when the different habitats are exploited provides needed information on ecological requirements for habitat management; recognition and protection of important habitats are necessary for effective fisheries management. Similarly, further descriptions of the different habitats are required to adequately assess the relative importance of habitat features to the different life-history stages of rockfishes. This study was designed to provide a quantitative comparison of habitat use for copper, quillback, and brown rockfishes on four habitat types common in Puget Sound.

Materials and methods

Study sites

For each of four habitat types—high-relief rocky reef, low-relief rocky reef, high-relief artificial reef, and sand/eelgrass—two representative replicate study sites were selected. The two high-relief natural rocky reefs were characterized by steep vertical relief to 5 m off the bottom, surface canopies of the annual bull kelp *Nereocystis leutkeana* May through November, and understories of the perennial kelps *Agarum fimbriatum* and *Pterygophora californica*. The high-relief rocky reefs range in depth from 12–20 m (gauged from mean lower low water). The Orchard Rocks high-relief rocky reef (HR1) is located on the southeastern side of Bainbridge Island (Fig. 1) approximately 600 m offshore in the middle of Rich Passage, which is swept by high currents up to 8.1 km/hour (4.5 knots) (U.S. Dep. Commer. 1987, current tables). The entire Orchard Rocks reef covers approximately 5 ha. The portion of reef used as the study site was about 12–18 m in depth and consisted of large boulders and rocky ledges that rise up to 5 m off the bottom. The second high-relief reef (HR2), Blakely Point, is a series of rock outcroppings separated by sand and shell gravel. The outcroppings are oriented perpendicularly offshore from the north entrance of Port Blakely Harbor on the eastern side of Bainbridge Island. Transects extended across the reef from 12–18 m in depth; each transect covered a similar depth range. Similar to HR1, the HR2 reef consists of steep walls and crevices with vertical relief of 5 m, but has minimal current.

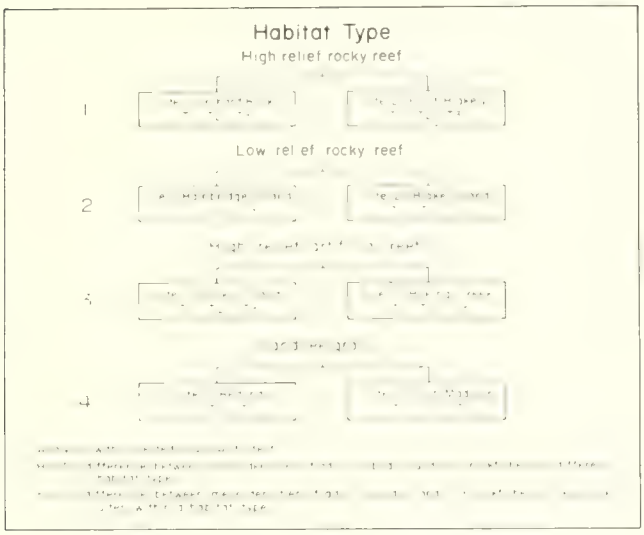

Figure 2
Nested experimental design showing habitat types in central Puget Sound, sites within habitat types, and the three transects per site.

The two low-relief rocky reefs were characterized by flat, featureless cobble and rock bottom with a few isolated areas of vertical relief (1–2 m). Transects extended from 8–10 m in depth, but not deeper than 10 m where the reef drops off into sand/cobble substrate. The low-relief reefs were more uniform in depth when compared with the high-relief reefs. Both low-relief reefs have dense canopies of *Nereocystis leutkeana* May through November and understories of perennial kelps *Agarum fimbriatum* and *Pterygophora californica*. Low-relief habitats underwent dramatic changes in the fall and winter when they were virtually devoid of all fish and algal structure. Bainbridge Island low-relief rocky reef (LR1) is 500 m inshore from HR1, and the two reefs are separated by cobble and sand. Blake Island low-relief reef (LR2) is located 5 km south of Bainbridge Island. Both low-relief reefs are swept by high currents up to 8.1 km/hour (4.5 knots).

The two high-relief artificial reefs were characterized by vertical relief of up to 5 m and no surface canopies of bull kelp, but with isolated patches of understory kelps. Transects extended from 15–20 m in depth. The Blake Island artificial reef (AR1) was constructed in 1980 (Laufle 1982) and is located 5 km south of Bainbridge Island on the southwestern side of Blake Island approximately 500 m offshore of LR1. The reef consists of concrete rubble, slabs, rectangular boxes, and tires forming vertical relief up to 4 m. The Boeing Creek artificial reef (AR2) was constructed in late 1982 and is located 8 km north of Shilshole marina approximately 600 m offshore. The reef consists of concrete rubble with vertical relief of up to 6 m. The two reefs differ, as Blake Island is swept by strong currents up to 8.1 km/hour (4.5 knots) while Boeing Creek experiences little current.

The sand/eelgrass areas were characterized by flat, shallow, unconsolidated substrate with dense growth of eelgrass *Zostera marina* May through November. Eelgrass typically grows in low-current, sheltered water and is restricted to depths less than 6 m (Phillips 1984), so the transects were placed at 5 m. The Redondo (SE1) sand/eelgrass area is located approximately 500 m north of Saltwater State Park, 24 km south of Seattle. The Port Madison eelgrass area (SE2) is located 500 m north of the Suquamish boat ramp, off the northern side of Bainbridge Island.

Survey methods

From December 1986 through February 1988, I conducted monthly SCUBA surveys and estimated rockfish densities along three (30-m long, 3 m wide, and 1 m high) permanent transect lines at each of the eight reefs (Fig. 2). After the February 1988 survey, surveys were conducted in April, June, July, and August of 1988. In October 1988, surveys quantifying only YOY rockfishes were conducted on four reefs where YOY had been observed in the summer and fall of 1987: HR2, LR1, AR2, and SE2. All eight sites were sampled each month, and all three transects were sampled on the same day. I swam along the transect line and recorded individuals of each species as YOY (<80 mm TL), subadult (80–200 mm TL), and adult (>200 mm TL). During the summer and early fall when kelp cover was the highest, I also swam through the canopy to search for YOY rockfish. The ability to designate these size categories was verified by periodically capturing and measuring fish. Because YOY copper, quillback, and brown rockfishes could not be identified to species underwater, they were combined into one group. A total of 456 transects was completed on all reefs: 24 transects conducted monthly for 15 consecutive months December 1986–February 1988, and 24 transects conducted monthly during April, June, July, and August 1988. Fifteen additional YOY surveys were completed in October 1988.

Other information collected along the transect lines included estimates of vegetative cover and water temperature. Kelp and eelgrass cover was qualitatively assessed by estimating, at the end of each transect, the percent cover of bullkelp, understory kelps, and the height of eelgrass present. The percent cover ranged from 0 (no vegetation present) to 100% (transect line completely covered by vegetation). Temperatures were recorded along the transect lines on each survey with a submersible thermometer.

Survey analyses

From the three transects at each site, a mean number (±95% CI) of fish per transect was computed for each species and size category. To determine whether densities of rockfishes differed among the four habitat types and within the two replicate sites within each habitat type, I used a nested analysis of variance (ANOVA) (Zar 1984) (Fig. 2) that tested two null hypotheses: (1) There is no difference in rockfish densities between habitats ($F_{0.05(1)3\text{(habitat types)},4\text{(sites)}}$), and (2) there is no difference in rockfish densities between the two replicate sites within each habitat type ($F_{0.05(1)4\text{(sites)},16\text{(error)}}$). The degrees of freedom for error was calculated as (4(types) · 2(sites) · 3(transects) – 4 · 2) = 16 (Zar 1984, p. 147). To reduce the number of analyses, data were analyzed as a separate ANOVA for each of six seasonal periods using the middle month: Winter 1 = December 1986–February 1987; spring = March 1987–May 1987; summer 1 = June 1987–August 1987; fall = September 1987–November 1987; winter 2 = December 1987–February 1988; and summer 2 = June 1988–August 1988. Although density estimates were similar within quarters (Figs. 3–6), the sedentary behavior of rockfish could mean that the same individuals were counted in February that had previously been counted in January, which would constitute a repeated sample. Thus to eliminate the possibility of non-independence of data, as I have no evidence that rockfish redistribute themselves randomly from month to month, I used only the middle month of each quarter. Because many months and sites contained zero densities and, in some cases, the variances were proportional to the means, the data were transformed using a square root transformation (X' = square root (X + 0.5)). If a significant difference in densities was detected among the four habitat types, the types were then compared using Tukey's multiple range test (Zar 1984) to determine which types were different.

To determine whether densities were different between years at each site, quarterly estimates were compared using a Student's t-test (Zar 1984). For these tests, densities from the summer of 1987 were compared with the summer of 1988 for each site testing the null hypothesis: There is no difference between densities of each site between summer 1987 and summer 1988. Similarly, densities from the winter of 1987 were compared with the winter of 1988. I conducted individual tests for copper, quillback, brown, and YOY rockfishes for summer and winter comparisons.

Results

Habitat type and site comparisons

All size categories of copper, quillback, and brown rockfishes and YOY rockfish were seen at the high-relief natural habitat type (Fig. 3). Consistent monthly densities of large (>200 mm) copper (mean 3.7–13.0 fish/90-m^3 transect) and quillback (mean 3.0–7.0 fish/transect) rockfishes were observed throughout the year on the high-relief rocky reefs. Brown rockfish (>200 mm) (mean 1.3–4.0 fish/transect) were seen at HR1 (Orchard Rocks) but infrequently at HR2 (Blakely Point). Low densities (mean<1.3 fish/transect) of subadult (80–200 mm) copper, quillback, and brown rockfishes were observed on both reefs until the late summer and fall 1987. YOY (<80 mm) rockfishes were observed (mean 8.0–57.0 fish/transect) from August–November 1987 but only on HR2. YOY were not observed in the summer or fall of 1988. After the influx of YOY during summer and fall 1987 on HR2, an increase in 80–200 mm rockfishes was subsequently observed (mean 6.0–15.0 fish/transect).

Rockfishes primarily utilized low-relief rocky reefs during the summer, coincident with peak *Nereocystis leutkeana* and understory cover, and were infrequently observed during other seasons (Fig. 4). Large copper (up to a mean 6.0 fish/transect) and brown rockfishes (up to a mean 7.7 fish/transect) were observed mainly during the summer, whereas large quillback rockfish were not seen at LR1 and only infrequently at LR2. Low densities (mean 0–3.3 fish/transect) of small copper and quillback rockfishes were seen on LR2, while small brown rockfish were never seen on either reef. YOY rockfishes were observed (mean 16.7 fish/transect) during August 1987 on LR1 and (mean 1.3 fish/transect) on LR2 during October 1987, but not during the summer or October of 1988.

On the artificial reefs, densities of large copper rockfish fluctuated throughout the year. During both 1987 and 1988, high densities (mean 12.0–56.3 fish/transect) were seen September through May; however, low densities (mean 0.3–2.3 fish/transect) of copper rockfish were observed June through August (Fig. 5). Variable densities (mean 0–12.3 fish/transect) of large quillback rockfish were observed on AR1 while they were lower in number (mean 0–2.3 fish/transect) on AR2 (Fig. 5). Large brown rockfish were infrequently (mean 0–0.3 fish/transect) seen on either artificial reef. Low densities (mean 0–5.0 fish/transect) of subadult (80–200 mm) copper rockfishes were observed on both artificial reefs throughout the year. Extremely high densities (mean 8.0–420.0 fish/transect) of subadult quillback rockfish were observed on both AR1 and AR2, although densities were much higher on AR2 (up to 420

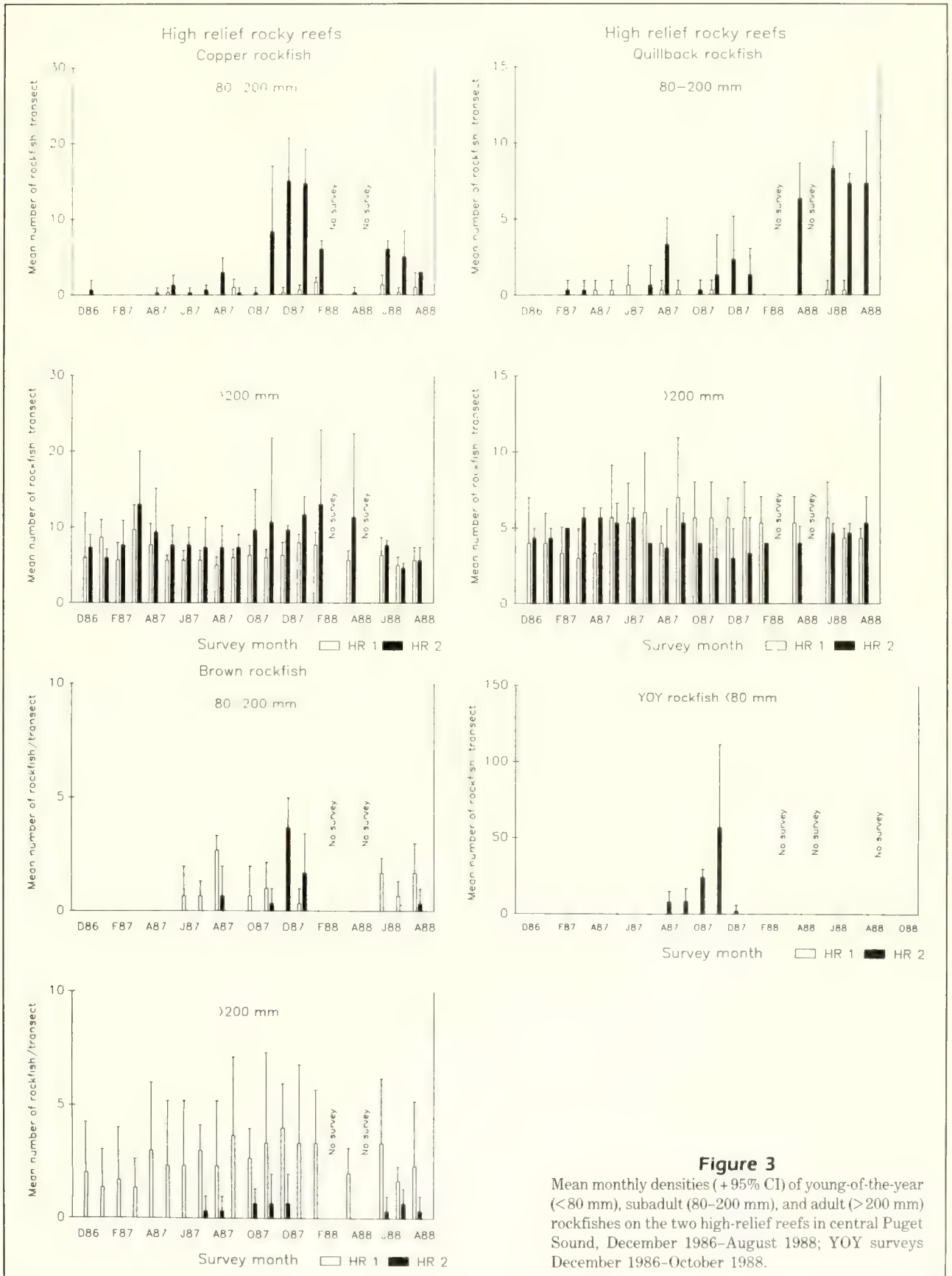

Figure 3

Mean monthly densities (+95% CI) of young-of-the-year (<80 mm), subadult (80–200 mm), and adult (>200 mm) rockfishes on the two high-relief reefs in central Puget Sound, December 1986–August 1988; YOY surveys December 1986–October 1988.

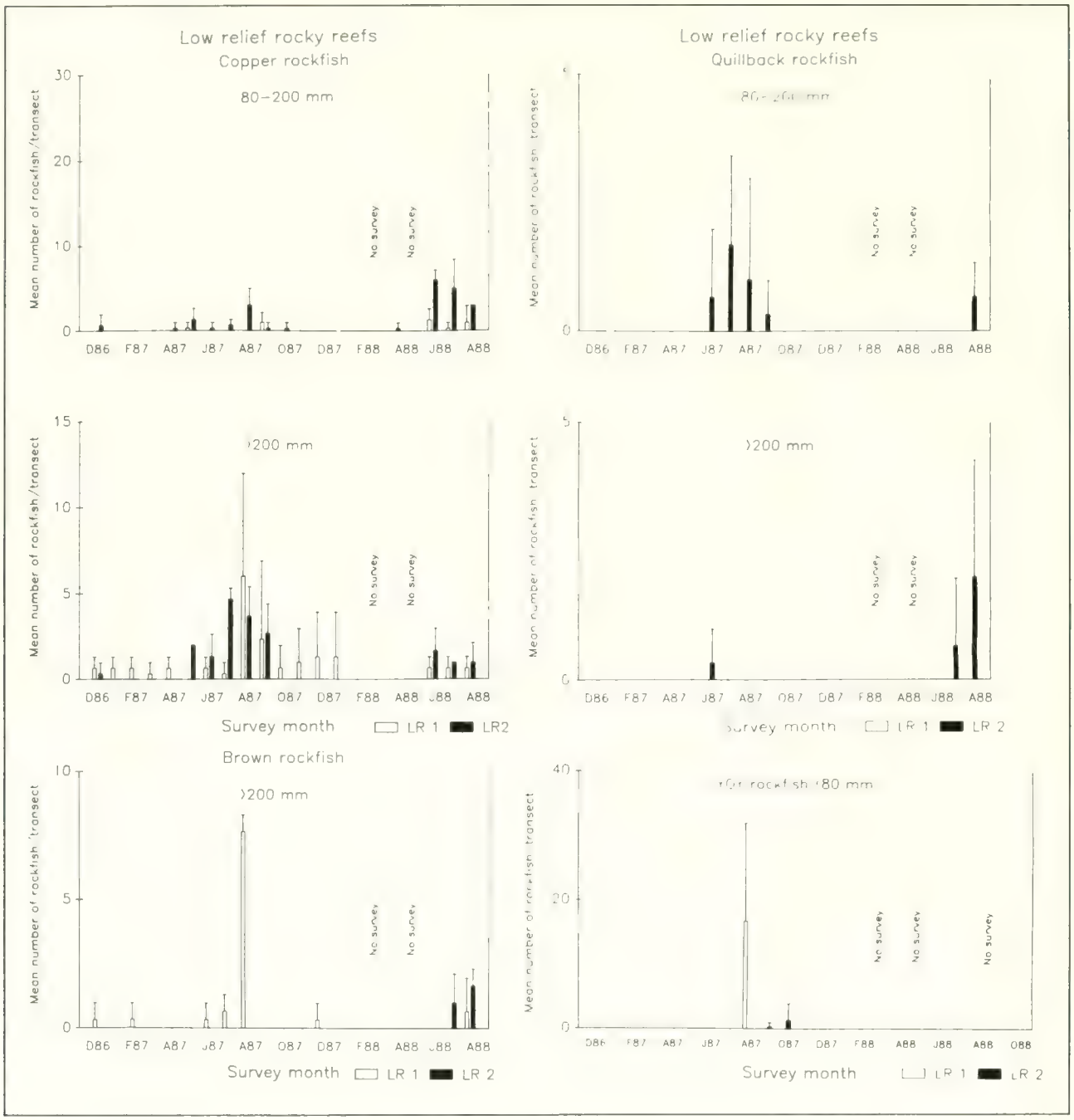

Figure 4

Mean monthly densities (+95% CI) of young-of-the-year (<80 mm), subadult (80–200 mm), and adult (>200 mm) rockfishes on the two low-relief reefs in central Puget Sound, December 1986–August 1988; YOY surveys December 1986–October 1988. No subadult brown rockfish were observed.

fish/transect). Small brown rockfish were infrequently (mean 0–0.3 fish/transect) seen on either artificial reef. YOY rockfishes were observed (mean 1.7–63.0 fish/transect) only on AR2 during the spring of 1987, and during the following fall, winter, spring, and summer (mean 4.3–80.0 fish/transect). Low densities (mean 2.0 fish/transect) were observed in the October 1988 survey. YOY were never observed on AR1.

Sand/eelgrass areas had the lowest densities of all habitats sampled; large copper rockfish (mean 5.0 in July 1987, mean 0.7 in August 1988), brown rockfish (mean 1.0, August 1987) and YOY (mean 111.0, July

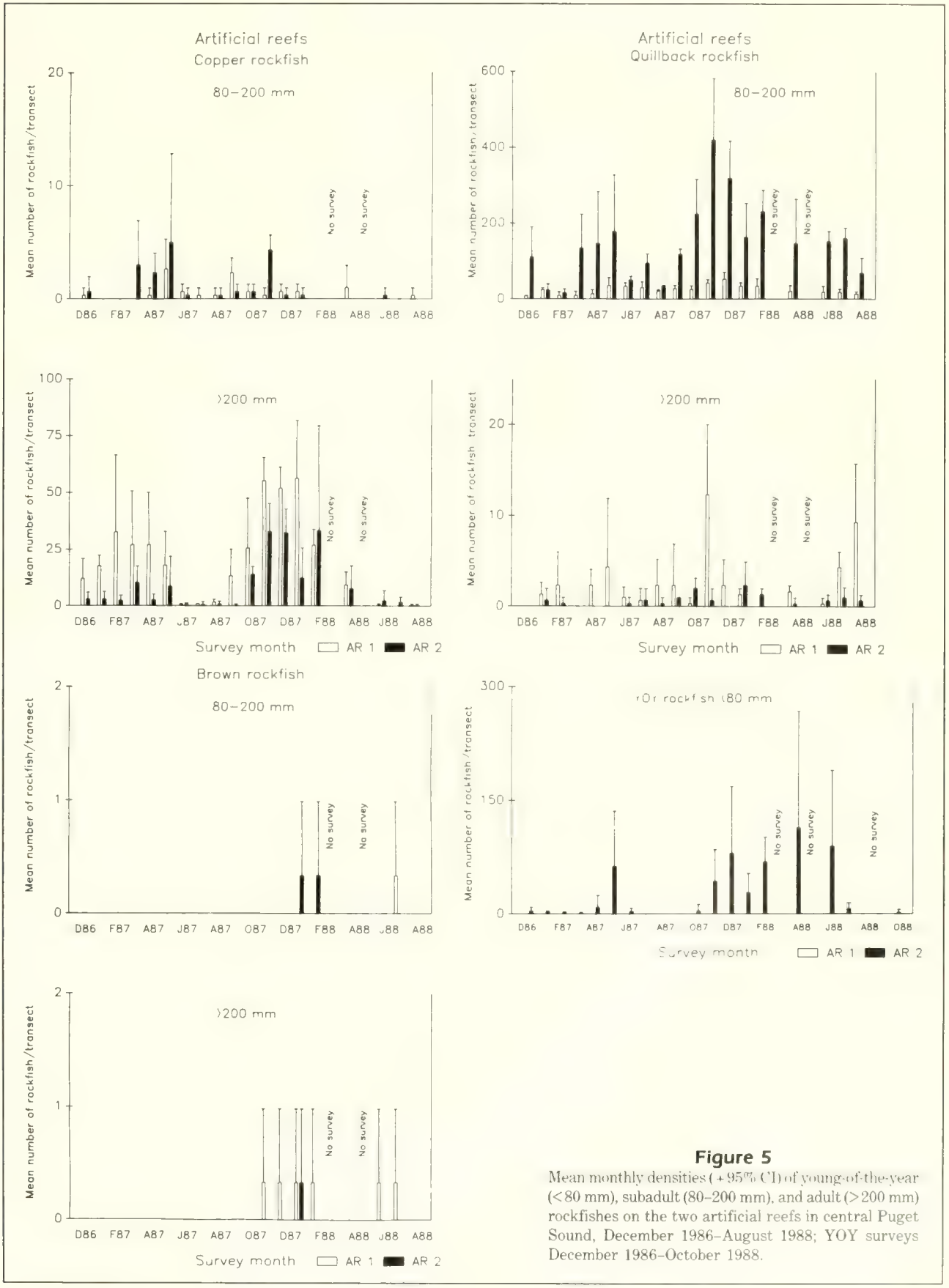

Figure 5

Mean monthly densities (+95% CI) of young-of-the-year (<80 mm), subadult (80–200 mm), and adult (>200 mm) rockfishes on the two artificial reefs in central Puget Sound, December 1986–August 1988; YOY surveys December 1986–October 1988.

1987) were the only rockfishes seen and only during surveys conducted in late July and August (Fig. 6). These observations of rockfishes coincided with the peak growth of eelgrass up to 1.5 m high; in the fall and winter the height of eelgrass beds was reduced to <0.5 m. No quillback rockfish were ever observed on sand/eelgrass.

Nested analysis of variance

Habitat type comparison When density differences were detected, the highest densities were observed on the high-relief rocky and artificial reefs ($P<0.05$ nested ANOVA, Table 1). Highest densities of large copper rockfish were observed on high-relief rocky reefs during both the summer of 1987 and 1988, whereas artificial reefs had the highest densities in the fall and winter. Similar low densities of 80–200 mm copper rockfish were observed on all four habitat types all seasons except fall 1987. High-relief rocky reefs had the highest densities of large quillback rockfish all seasons; sand/eelgrass and low-relief rocky reefs were similar as large quillback rockfish were rarely observed. Artificial reefs had the highest densities of 80–200 mm quillback rockfish all seasons except winter and summer 1988. No density differences were observed for both size groups of brown rockfish on any of the habitat types. Similarly, YOY rockfishes were observed on all four habitat types, and no differences were detected in densities of YOY rockfish among the four habitats.

Replicate site comparison For many (23/42 groups) size groups of copper, quillback, brown, and YOY rockfishes, there were significant differences in densities between the two replicate sites for most seasons ($P<0.05$ nested ANOVA, Table 1). The major exception was that similar densities of large copper rockfish were observed on replicate sites all seasons except spring 1987.

Year-to-year comparison

For most size categories of copper, quillback, and brown rockfishes, there were no significant difference between their densities for the two periods tested: Summer 1987–summer 1988, and winter 1987–winter 1988 (Table 2). For the summer comparisons, the principal differences in densities were for YOY rockfish on all sites where they were observed: HR2, LR1, LR2, AR2, and SE2. YOY were observed at all five reefs in the summer of 1987; however, no YOY were observed in the summer of 1988, except at AR2. Other differences between summer 1987–1988 densities were 80–200 mm quillback rockfish on HR2; densities of small quillback rockfish were higher in the summer of 1988 after the YOY recruitment of 1987.

Similar to the summer 1987–summer 1988 comparisons, there were few significant density differences for winter 1987–winter 1988 (Table 2). The principal differences were that large copper rockfish and small

Figure 6

Mean monthly densities (+95% CI) of young-of-the-year (<80 mm), subadult (80–200 mm), and adult (>200 mm) rockfishes on the two sand/eelgrass areas in central Puget Sound, December 1986–August 1988; YOY surveys December 1986–October 1988. No quillback rockfish (80–200 mm or >200 mm), subadult copper rockfish, or subadult brown rockfish were observed.

Table 1

Results of the nested ANOVAs ($P<0.05$) testing for differences between rockfish densities among the four habitat types: High-relief rocky reef (HR), low-relief rocky reef (LR), high-relief artificial reef (AR), and sand eelgrass (SE). If there was a significant difference between type densities (Test 1), the results of Tukey's multiple range test are listed from highest to lowest densities. Test 2 lists the significant differences (*) in densities between sites.

	Copper		Quillback		Brown		Young-of-the-year
	80–200	>200 mm	80–200 mm	>200 mm	80–200 mm	>200 mm	<80 mm
Test 1							
1987							
Winter			AR>HR>SE=LR	HR>AR>LR=SE			
Spring			AR>HR>SE=LR	HR>AR>LR=SE			
Summer		HR>LR>AR=SE	AR>HR>SE=LR	HR>AR>LR=SE			
Fall	AR>HR>LR=SE	AR>HR>LR=SE	AR>HR>SE=LR	HR>AR>LR=SE			
1988							
Winter		AR>HR>LR=SE		HR>AR>LR=SE			
Summer		HR>LR>AR=SE		HR>AR>LR=SE			
Test 2							
1987							
Winter							*
Spring	*	*	*	*		*	
Summer			*		*	*	*
Fall			*	*		*	*
1988							
Winter	*		*			*	*
Summer	*		*	*		*	*

Table 2

Summary of year-to-year comparisons testing (Student's t-test) for differences in rockfish densities between summer (June, July, Aug.) 1987–summer 1988 and winter (Dec., Jan., Feb.) 1987–winter 1988. Listed are habitat types where a significant difference was detected. HR = high-relief rocky reef, AR = high-relief artificial reef, LR = low-relief rocky reef, SE = sand/eelgrass.

	Summer 1987–Summer 1988	Winter 1987–Winter 1988
Copper		
80–200 mm	HR2	HR2
>200 mm	AR1	HR2, AR1, AR2
Quillback		
80–200 mm	HR2, AR1, AR2	AR1, AR2
>200 mm	No differences	HR1
Brown		
80-200 mm	No differences	HR2
>200 mm	LR1	No differences
Young-of-the-year		
<80 mm	HR2, LR1, LR2, AR2, SE2	AR2

quillback rockfish densities were higher in the winter of 1988 on both artificial reefs. In addition, both small and large copper rockfish increased on HR2.

Species comparison

Small copper rockfish were infrequently seen on any habitat (Figs. 3–6). Small copper rockfish were first observed on the high-relief rocky reefs after the influx of YOY in the fall and winter. They were also sporadically observed on the artificial reefs and Blake Island low-relief reef. Large copper rockfish were seen on all habitat types and were observed all seasons. Consistent densities of large copper rockfish were observed

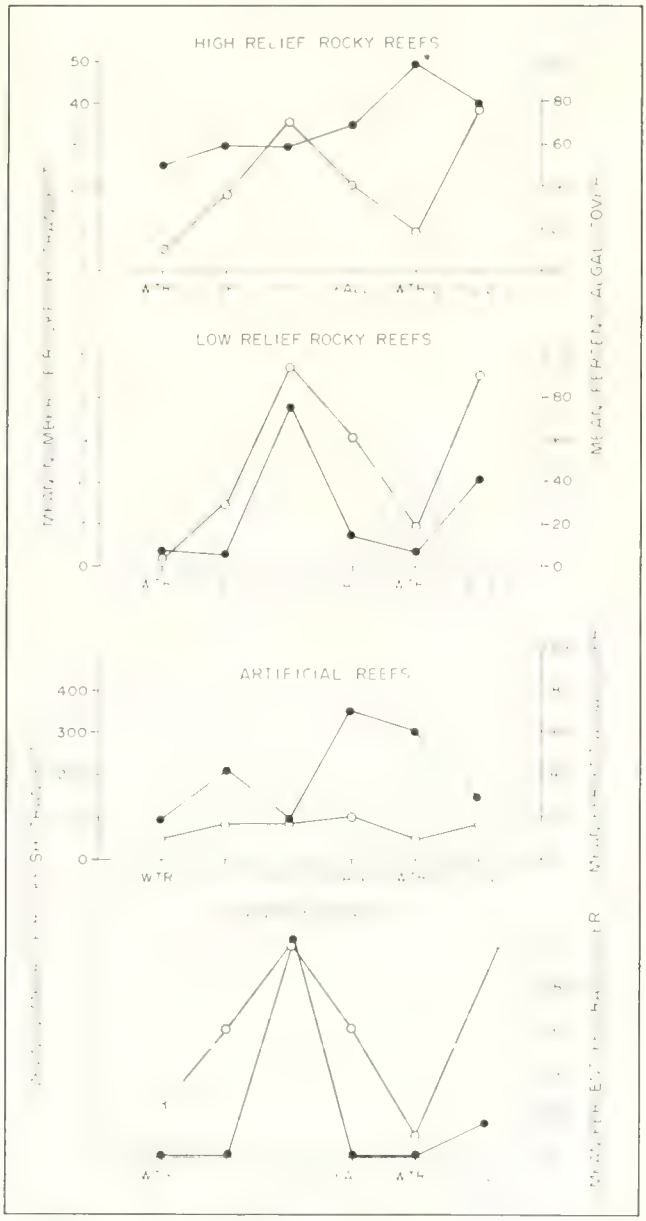

Figure 7

Mean percent of algal or eelgrass cover (○) compared with mean number (●, combination of 80–200 mm and >200 mm) of copper, quillback, and brown rockfishes on the four habitat types in central Puget Sound for winter 1 (wtr1), spring (sp), summer 1 (su1), fall (fall), winter 2 (wtr2), and summer 2 (su2). Seasons are described in Methods section. Density increase in high-relief rockfish (*) followed the influx of young-of-the-year rockfish. Percent eelgrass cover was relative to maximum height (1.5 m) of eelgrass which occurred during the summer.

on the high-relief reefs all seasons. In contrast, their densities fluctuated seasonally on other habitats; they were only observed during the summer and fall on the low-relief reefs during all seasons, although in lower densities during the summer on the artificial reefs, and only during the summer on the sand/eelgrass.

Small quillback rockfish were primarily observed on the artificial reefs all seasons and were infrequently observed on all other habitats (Figs. 3–5). Large quillback rockfish were most common on the high-relief rocky reefs and artificial reefs. Large quillback rockfish were rarely observed on the low-relief reefs. Neither small nor large quillback rockfish were observed on the sand/eelgrass.

Small brown rockfish were observed only on the high-relief reefs and on one artificial reef (Figs. 3, 5). Large brown rockfish were seen all seasons on the high-relief reefs although highest numbers were observed at HR1 (Orchard Rocks) (Fig. 3). They were also seen during the summer on low-relief reefs and sand/eelgrass (Figs. 4, 6).

YOY rockfish were observed on all four habitat types (Figs. 3–6). On the high-relief, low-relief reefs, and the sand/eelgrass, they were first seen in the summer and fall of 1987. YOY were observed year-round on Boeing Creek artificial reef. YOY were not observed in the summer or October of 1988 except at AR2.

Macrophyte cover varied seasonally; the densest cover was observed June through October on all reefs (Fig. 7). The high-relief reefs had dense canopies of *Nereocystis leutkeana* and subcanopies of *Pterygophora californica*, and *Agarum* that during the summer covered 50–100% of the bottom along the transect lines. The two low-relief reefs had 100% bullkelp and understory coverage June through October. The annual bullkelp was gone November through May and only the stipes of the understory perennial kelps remained; the blades of the understory kelps had eroded or were otherwise lost. There was no *Nereocystis* on the two artificial reefs; however, understory kelps covered approximately 0–20% of the transects, with peak growth in the summer. Sand/eelgrass transects were always covered with the perennial eelgrass throughout the year, although the height varied seasonally. The height peaked during the summer at approximately 1.5 m, and during the winter many of the blades were gone and the eelgrass was prostrate with little (0–0.5 m) vertical structure.

Monthly mean temperatures were highest August through October (up to 13°C) and lowest (down to 7.1°C) in January and February (Fig. 8). There was little qualitative difference in temperatures between the different reefs, although depth ranges were 5–20 m along transect lines.

Discussion

Seasonal habitat use

Habitats that underwent seasonal vegetation and subsequent structural changes had the most dramatic

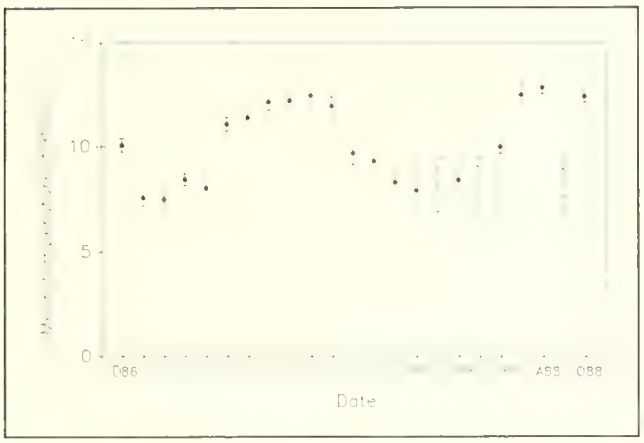

Figure 8

Mean monthly bottom temperatures (°C) ±95% CI measured along transect lines on the eight reefs in central Puget Sound, December 1986–October 1988.

density differences (Fig. 7). On the low-relief rocky reefs and sand/eelgrass, the highest densities, mainly >200 mm copper, brown, and YOY rockfishes, were observed during the summer coincident with the densest growth of bull kelp, understory kelps, and eelgrass. When the vegetation died back, lowest densities of rockfishes were observed, presumably due to movement away from the reefs. Movement away from the Blake Island low-relief reef in the fall onto the Blake Island artificial reef was confirmed in a tag-recapture study (Matthews In press). Richards (1987) also noted a decrease in copper rockfish densities off Vancouver Island during the winter, but argued that it was not fish movement that caused the decrease in densities but rather that during the winter fish were simply more difficult to see as they presumably hid in crevices. On the low-relief reefs and sand/eelgrass areas I surveyed, this explanation was not the case. Once the vegetation died back there were few places for fish to hide undetected by divers; there are no crevices or holes in the flat-bottom rock reef and sand. Fishing pressure was not responsible for the seasonal density fluctuations. Although I never directly measured the amount of fishing activity, I observed the highest number of sportfishing boats (both divers and anglers) at the high-relief reefs, whereas the lowest fishing effort occurred at the low-relief and artificial reefs. Larson and DeMartini (1984) compared two low-relief areas in southern California with and without giant kelp *Macrocystis pyrifera*. They found a higher biomass of fishes on the reef with kelp and concluded that the presence of kelp on low-relief reefs enhances fish biomass by providing prey and structure. The seasonal change in kelp on high-relief reefs had no effect on fish densities; presumably there is adequate structure (rocks and crevices) and prey on these reefs regardless of kelp cover. Other research in California has demonstrated that kelp on high-relief reefs had less effect on fish abundance when compared with their dramatic effect on low-relief reefs; when kelp cover declines on low-relief reefs, the shelter is lost but refuge in high-relief rock is permanent regardless of kelp cover (Quast 1968, Stephens et al. 1984, Ebeling and Laur 1988). Large (>200 mm) copper rockfish densities on the artificial reefs declined dramatically during the summer coincident with higher densities of large copper rockfish on the low-relief rocky reefs. Copper rockfish may leave the artificial reefs in the summer because of the lack of vegetation (bullkelp and understory kelps) and its associated prey. The summer is an important feeding time for rockfishes when fat reserves are stored to be used as energy sources during the winter (Guillemot et al. 1985). Although the artificial reefs had isolated patches of perennial kelps (*Agarum* and *Pterygophora*) during the summer, this habitat type had the sparsest vegetation growth of all the habitats surveyed. Because low-relief rocky reefs, artificial reefs, and sand/eelgrass were not suitable year-round habitats, rockfish move to utilize alternate habitats during the winter (Matthews In press).

Habitat comparison

Apparently, high-relief rocky reefs were suitable habitat for copper, quillback, brown, and YOY rockfishes: This was the only habitat type where all size categories of the three species as well as YOY were observed, although few were observed in the 80–200 mm range. Actually, one should not expect to see high numbers of 80–200 mm rockfish. Copper and quillback rockfishes are relatively slow-growing and may live up to 55 years (Richards and Cass 1987). Rockfishes release thousands of larvae, and the highest predation and mortality is on the youngest fish; presumably only a few survive to adults. Rockfish >200 mm represent several age groups—those rockfish about 5 years and older—whereas the 80–200 mm group represents only a few age classes of 1–5 years (Sandra Oxford, Wash. Dep. Fish., Seattle, WA 98115, pers. commun., summer 1988). Thus, one would expect to see more fish >200 mm than 80–200 mm on the high-relief natural reefs where the size groups co-occur. High-relief rocky reefs also had the most consistent densities of large rockfish and were the most structurally complex of all habitats surveyed. Although the vertical relief was similar to that on artificial reefs, natural rocky reefs had more cracks, crevices, and holes for fish to hide. Moreover, the algal diversity and cover was considerably greater; thus high-relief rocky reefs provided the most structurally diverse and persistent habitat.

Low-relief rocky reefs and sand/eelgrass were temporary habitats primarily utilized during the summer, coincident with summer vegetation growth. Presumably rockfishes utilize these habitats when structure and prey availability are highest and subsequently move to other more suitable habitats (Matthews In press). Although rockfish densities were low, these habitats cover considerably more area than artificial reefs or high-relief rocky reefs in Puget Sound, and thus are important to rockfish.

The highest densities of rockfishes were observed on the artificial reefs, primarily 80–200 mm quillback rockfish. Artificial reefs had high densities of 80–200 mm quillback rockfish throughout the year, although some fluctuations occurred, and high densities of large copper rockfish in the fall, winter, and spring. No other reefs surveyed had such high densities of 80–200 mm rockfishes of any species, and it is not known whether this results from higher survival of small quillback rockfish on artificial reefs. Furthermore, it is puzzling that more large quillback rockfish were not found on the artificial reefs, considering the abundance of 80–200 mm quillback rockfish. Several hypotheses could explain the low numbers of large quillback rockfish on the artificial reefs: (1) Artificial reefs are not suitable habitat for large quillback rockfish, i.e., they leave when they grow large; (2) the fish have not yet grown to the larger size; (3) some factor is preventing the fish from growing; or (4) there is a high mortality of fish once they reach the 200-mm size. I ruled out the possibility that large copper rockfish competitively excluded large quillbacks, as the two species coexist on high-relief natural reefs, although competition may be reduced at high-relief habitats if resources are not limiting. The shortage of large quillback rockfish on the artificial reefs is not depth-related since large quillbacks have been observed at similar depths in other studies (Moulton 1977, Richards 1987) and at HR1 and HR2. Again, the lack of large quillback rockfish was not due to fishing pressure: I observed low levels of fishing at both artificial reefs. Furthermore, if fishing pressure was responsible for the lack of large fish, there would be few large copper rockfish. In any case, this apparent refuge for 80–200 mm quillback rockfish should be investigated to determine if rockfish leave once they reach a certain size and eventually contribute to recreational fisheries. Although it has been well established that artificial reefs attract high densities of fish, in this case 80–200 mm quillback rockfish, there is no information that verifies whether there is adequate food or if growth or mortality is similar to that observed on natural reefs (Ambrose and Swarbrick 1989).

Year-to-year comparison

In a 4-year study of kelp-bed fishes in southern California, Ebeling et al. (1980) found little annual variation in numbers of bottom assemblages, including rockfishes. Although my study demonstrated significant seasonal changes within a habitat (artificial reefs, low relief, sand/eelgrass), when analyzed between seasons there were few differences between years, with the exception of YOY. Ebeling et al. (1980) suggested that the low annual variation in kelp-bed fish assemblages was characteristic of stable communities in predictable environments. Although more recent work (Ebeling and Laur 1988) demonstrated the dramatic effect storms can have on fish populations, Puget Sound is a relatively protected environment not subjected to open ocean waves and surge. Thus year-to-year variation in Puget Sound rockfish populations may be small.

Species comparison

Copper rockfish occurred on all habitats and can be considered a habitat generalist. Large copper rockfish were observed on all four habitats, although they left the artificial reefs in the summer and moved into shallower low-relief and sand/eelgrass areas. Buckley and Hueckel (1985) also noted a seasonal decrease of copper rockfish densities during the summer on Gedney Island artificial reef in central Puget Sound, and highest densities were noted during the fall and winter. They speculated rockfish movement was in response to prey occurrence (surfperch). Moulton (1977) speculated that copper rockfish move to deeper water during the fall in northern Puget Sound due to seasonal depth preference or prey availability. Turbulence presumably does not contribute to movement; in Puget Sound most water motion on the bottom is from currents, not surge or turbulence, and water motion is similar in the summer and winter. In the summer, copper rockfish utilized several habitats: high-relief rocky reefs, low-relief reefs, and sand/eelgrass. Their appearance on the shallower reefs during the summer and disappearance from the deeper artificial reefs is not simply a shallower depth preference in the summer; copper rockfish were observed during the summer at the high-relief reefs even at comparable artificial reef depths.

Quillback rockfish were more restricted in their distribution when compared with copper rockfish. Similarly, quillback rockfish were not as widely distributed as copper rockfish at 12 study sites in the Strait of Georgia (Richards 1987). The small quillback rockfish were seen in very high densities on the artificial reefs, but infrequently on other habitats. Large quillback rockfish were primarily seen on high-relief rocky and artificial

reefs; Richards (1987) noted quillback rockfish densities were correlated with relief, and highest densities were found on complex habitats. The lack of large quillback rockfish on low-relief and sand/eelgrass areas is presumably due to their preference for high relief and complex habitats.

Brown rockfish displayed the most restricted and perplexing distribution, primarily being found on Orchard Rocks high-relief reef and the inshore low-relief reefs during the summer, and rarely observed on artificial reefs or sand/eelgrass. Brown rockfish have been observed on artificial reefs in south Puget Sound (Greg Hueckel, Wash. Dep. Fish., Olympia, WA 98504, pers. commun., summer 1988) and it is unclear why they did not inhabit the artificial reefs in central Puget Sound. Additionally, brown rockfish are relatively uncommon on rocky reefs in northern Puget Sound and the San Juan Islands (Moulton 1977). In California, brown rockfish are primarily found on sandy, low-relief areas (Matthews 1985); their different habitat use in Puget Sound could be due to local hybridization with congeners (L. Seeb, Southern Ill. Univ., Carbondale, IL 62901, pers. commun., summer 1987).

YOY were distributed differentially among all habitat types. The sand/eelgrass was a temporary YOY habitat, as YOY were observed in July and never again seen. Either the YOY left the area or died. Similarly, YOY were observed on the low-relief reefs but subsequently emigrated or suffered high mortality; their contribution to recruitment on other reefs is unknown. On the other hand, YOY were first observed on the transects on HR2 in August, although they were previously seen in July off the reef on adjacent (within 25 m) sand/*Agarum*. The numbers of YOY increased over the next few months, peaked in November, and initial settlement was followed by an increase in the 80–200 mm copper, quillback, and brown rockfishes, presumably, the result of recruits staying and growing into the larger size category. A similar pattern of YOY influx was followed by an increase in the 80–200 mm group on AR2, although two periods of YOY settlement were observed, spring and fall.

Parturition of these rockfishes reportedly occurs April through June, as most female rockfishes captured April and May near Bainbridge Island had embryos and ovaries that were in the transitional stage during the summer (DeLacy et al. 1964, Washington et al. 1979, Dygert 1986). On SCUBA surveys, I saw pregnant rockfish late April through late June. Therefore, the YOY that were observed during the summer and fall of 1987 on HR2 presumably were released between April and July, spent some unknown amount of time in pelagic regions or on some other habitat, and then settled to a demersal existence in July and August. Examinations of the otolith microstructure of eight 45–60 mm TL rockfish (M. Yoklavich, Natl. Mar. Fish. Serv., Seattle, WA 98115, pers. commun., fall 1987) that I collected 29 August 1987 on HR2 revealed approximately 120–160 growth rings. Similar growth rings have been shown to be deposited daily in black rockfish (Yoklavich and Boehlert 1987). If the rings examined on my rockfish were also daily, it would confirm that parturition occurred around April. Additionally, these fish appeared to grow quite quickly. When first observed in July and August they were approximately 45–60 mm TL and by November were 90–100 mm TL (fish were captured to verify these measurements). This scenario describes the parturition on the natural reefs which was quite different from the YOY settlement on Boeing Creek artificial reef. YOY were assumed to be primarily quillback rockfish, as YOY settlement was followed by an increase of 80–200 mm quillback rockfish. They were observed in the spring and the fall on Boeing Creek artificial reef. It is unclear when the spring recruits were released or if there are possibly two reproductive periods for quillback rockfish in Washington as noted for some California rockfishes (Wyllie Echeverria 1987). Brown rockfish sampled from one location in north-central California had two distinct seasons of larval extrusion, December and June, and Wyllie Echeverria (1987) concluded that rockfishes have a flexible reproduction system that enables individuals to adaptively respond to environmental factors. On the other hand, in my study young quillback rockfish could arrive from another source—northern Puget Sound, Strait of Juan de Fuca, or even the outer coast of Washington—causing the second pulse.

On Vancouver Island, Haldorson and Richards (1987) noted an influx of YOY (<50 mm) copper rockfish during August and September; the YOY utilized four habitat types: (1) *Nereocystis leutkeana*, (2) *Agarum* slopes, (3) eelgrass, and (4) sand. They observed the highest densities of young copper rockfish first in the bullkelp canopies. Subsequently, the young rockfish left the kelp canopy and were found on the floor of the kelp forest in September and October, coincident with fall storms and the annual decomposition of the bullkelp. After the initial association with the kelp canopy, the YOY shifted their distribution to a demersal habitat with the perennial macrophytes *Agarum* and eelgrass. Similarly, Carr (1983) first observed YOY copper rockfish in the upper canopy of giant kelp *Macrocystis pyrifera* in central California kelp beds. The YOY copper rockfish subsequently moved toward the bottom over the following weeks. Carr (1983) and Haldorson and Richards (1987) always observed YOY in close proximity to drift or attached kelp or eelgrass and suggested that young rockfishes strongly associated with plant cover to avoid predation and find food resources.

Interestingly, I never observed YOY in bullkelp canopy. The young fish were only seen on the bottom closely associated with the perennial understory macrophytes *Agarum*, *Pterygophora*, and eelgrass, or closely associated with rocks at AR2, which has little plant cover. The YOY could have spent a short period of time in the bullkelp canopy before I first saw them in my surveys or they may never use the bullkelp canopy in my study sites. Young rockfish may not be able to maintain position in the water column in areas with current.

It is not surprising that YOY rockfishes were seen in 1987, yet not in 1988. The numbers of first-year rockfish recruits reportedly vary greatly year-to-year along the coast of central and northern California (Hobson et al. 1986, Gaines and Roughgarden 1987). Studies in California have documented wide fluctuations in YOY recruitment sometimes influenced by warm-water years and changes in distribution after kelp removal (Bodkin 1988). Temperature did not appear to be a factor in the absence of YOY in 1988; bottom temperatures were similar between 1987 and 1988 (Fig. 8). In addition, few YOY were observed off eastern Vancouver Island during the same time period (summer and fall 1988) (L. Richards, Pac. Biol. Sttn., Nanaimo, B.C., Canada V9R 5K6, pers. commun., spring 1989). Apparently, copper, quillback, and brown rockfish recruitment is episodic; this has important implications to our understanding of the population dynamics and management of Puget Sound rockfishes.

The most numerous aggregations of YOY were observed on low-current reefs: HR2, AR2, and SE2. YOY were never observed on the highest current reefs, HR1 and AR1. Possibly YOY settle out on high-current reefs but lack the ability to remain on the reef and are swept away by strong current. In contrast, larvae may accumulate at sites of low current velocity. Leaman (1976) collected significantly higher numbers of *Sebastes* larvae in sheltered waters than in open, more exposed channels off the west coast of Vancouver Island. Similarly, Haldorson and Richards' (1987) observations of YOY rockfishes on eastern Vancouver Island were in low-current areas.

Experimental design

Because underwater transects are an effective means of describing large diurnally active fish populations (Brock 1954, Brock 1982), my transects were probably effective for estimating abundances of adult rockfishes, although I probably underestimated YOY rockfishes and the very dense aggregations of 80–200 mm quillback rockfish on the artificial reefs. For many size categories of the three species during most seasons, there were density differences between the two replicate sites (reefs) within each habitat type. This variability suggests there may not be a typical rocky reef or artificial reef. In most cases, though, this difference was due to variability in densities and not to different species present on the reef. For example, both AR1 and AR2 had very high densities of 80–200 mm quillback rockfish, perhaps a characteristic of artificial reefs in Puget Sound. High densities of 80–200 mm rockfishes were not observed on any other reef type, but AR2 had significantly larger densities, perhaps due to location or age of the reef.

Habitat quality

Which is the highest quality habitat? One view of habitat quality would predict that densities are directly proportional to quality; rockfish densities are highest where habitat quality is highest. This reasoning forms the basis of many current habitat assessment models in resource management (Van Horne 1983). In the absence of long-term information on growth, survival, stability, and other features of how species respond to different habitats, habitat quality is evaluated in short-term studies describing densities (Van Horne 1983). Those habitats with the highest densities will be those most important to the maintenance of that species and should ultimately be protected as critical habitat. It is important to note that densities can be misleading in designating habitat quality (Van Horne 1983). While my habitat surveys documented the highest rockfish densities on artificial reefs, the densities underwent major fluctuations. According to classic ecological theory, as density increases habitat quality declines (Svardson 1949, Fretwell 1972). If resources are limited, then at high rockfish densities, food, hiding, and resting places would be in short supply, thereby reducing growth and survival. In my study, changes in availability of resources presumably were the causes for rockfish density fluctuations. Therefore, a true measure of habitat quality should include factors other than densities, such as availability of essential resources, stability over time, survival, reproductive output, growth, and the animal's preference for that habitat. Nevertheless, copper, quillback, and brown rockfish utilized all four habitat types surveyed, and each habitat is important. But some of these habitats vary seasonally vary their suitability, and so rockfishes move to exploit alternate habitats when suitability is low (Matthews In press). Thus, for rockfishes, I would argue that high densities should not be the primary indicator of habitat quality, particularly in reference to the high ratio of small/large quillback rockfish on artificial reefs. Documenting densities of rockfishes only during a short time frame (few months) would not be representative of that habitat's importance. In addition, low-relief rocky reefs, although only important as

rockfish habitat in the summer, likely represent essential summer feeding area for rockfishes. Although densities are low, this habitat type is widespread in Puget Sound. In order to protect low-relief habitats, they would obviously have to be preserved year-round, i.e.. not altered or destroyed. Thus, in terms of seasonal stability in densities, presence of all size categories, and seasonal resource availability, I suggest the following ranks for the different habitats, listed from highest to lowest: High-relief rocky reefs, low-relief reefs (important as summer feeding area and thus contribute to year-round growth), artificial reefs (pending further research and assessment), and sand/eelgrass.

Regardless of which habitat has the highest quality, the habitat types examined in this study were utilized differently by the various size groups and species. Recently, however, Hueckel et al. (1989) have suggested that artificial reefs can be used as mitigation for the loss of natural rocky-reef habitat. Mitigating the loss of natural habitats with artificial reefs uses the rationale that artificial reefs provide rocky-reef type substrate that replicates natural rocky reefs. Hueckel and Buckley (1989) reported that artificial reefs in Puget Sound replicate processes on natural reefs and provide as evidence the similarity in the number of fish and prey species present on artificial and natural reefs. My research indicated that rockfish species composition was similar (with the exception of brown rockfish) between natural and artificial reefs. However, these species utilize artificial reefs quite differently than natural reefs: Large copper rockfish leave artificial reefs during the summer, large quillback rockfish are found in small numbers, and artificial reefs are dominated by extremely high densities of small quillback rockfish, unlike any natural reef I surveyed. In fact, the artificial reefs I studied seem to represent an anomalous habitat unlike any natural habitat.

Furthermore, the difference in resource availability and habitat use may result in different birth and death rates on different habitats. Thus, the different habitats could be viewed as sources, where reproductive output exceeds deaths, or sinks, where a deficit exists (Pulliam 1988). On the superficial observation of high densities of quillback rockfishes on artificial reefs, it could be determined that the destruction of a nearby rocky reef would have little impact on rockfishes. Pulliam (1988) points out that if a habitat (e.g., artificial reef) being preserved was a sink and the one being destroyed was a source (e.g., natural rocky reef), destruction of a relatively small source habitat could then have disastrous results. For example, if a low-relief natural reef was destroyed for a development project, the loss of the productive feeding area used by artificial-reef rockfishes during the summer could result in reduced growth and less reproductive output. Again, whether or not artificial reefs provide adequate food for such high densities of rockfishes is unknown. The largest rockfish inhabiting artificial reefs were those that made use of natural habitats; their movement was confirmed in a tagging study (Matthews 1988). Thus copper rockfish may be maintained by a source habitat when they make use of kelp beds during the summer. In addition, artificial reefs are considerably smaller than natural reefs, so they would not compensate for the total loss of abundance (Ambrose and Swarbrick 1989). Thus it is premature and speculative to suggest that artificial reefs should be used as mitigation.

Summary

Habitat surveys comparing monthly densities of copper, quillback, and brown rockfishes on high-relief rocky reefs, low-relief rocky reefs, high-relief artificial reefs, and sand/eelgrass areas demonstrated strong differences in how rockfishes utilize these habitats. High-relief rocky reefs had the most consistent densities of the three species of rockfishes, mostly fish >200 mm. Low-relief rocky reefs were primarily inhabited in the summer months coincident with the summer growth of *Nereocystis leutkeana*. YOY rockfishes were also observed on low-relief reefs; however, most fish left these reefs in the fall. The highest densities of rockfishes, primarily 80–200 mm quillback rockfish (up to 420/90-m^3 transect), were observed on artificial reefs and high densities of large copper rockfish were also observed. On artificial reefs, density fluctuations were dramatic; copper rockfish densities peaked in the fall and winter and declined (to 0/transect) during the summer and quillback rockfish densities also seasonally fluctuated. Brown rockfish were rarely seen on the artificial reefs. Sand/eelgrass areas were the least utilized habitat type; only during July and August were YOY, adult copper rockfish, and brown rockfish observed on one sand/eelgrass habitat. Although all four habitats were used, natural reefs may represent source habitats that are used by and maintain rockfishes on less productive sink (artificial reef) habitats. Thus the recent use of artificial reefs as mitigation for the loss of natural reefs could have negative impacts on rockfish populations.

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Separation of Two Species of Sand Lances, *Ammodytes americanus* and *A. dubius*, in the Western North Atlantic

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Abstract.–Two species of sand lances are recognized in the western North Atlantic, the inshore *Ammodytes americanus* DeKay 1842 and the offshore *A. dubius* Reinhardt 1838. The best separation of the two species is achieved by using the number of plicae (oblique folds of skin on the lateral body surface) singly or in combination with the number of vertebrae. *Ammodytes americanus* has fewer meristic structures than *A. dubius*: number of lateral plicae 106–126, $\bar{x}$ 117.4 vs. 124–147, 132.1; total vertebrae 62–70, $\bar{x}$ 66.4 vs. 68–76, 70.8; dorsal fin rays 52–61, $\bar{x}$ 57.4 vs. 56–67, 61.8; anal fin rays 26–33, $\bar{x}$ 29.4 vs. 28–35, 31.1; pectoral fin rays 11–15, $\bar{x}$ 13.2 vs. 12–16, 14.0; gill rakers on first arch 21–28, $\bar{x}$ 24.3 vs. 23–31, 26.6. Meristic differences between species were summarized with principle component analysis. In addition to considerable variation within samples, there is geographic variation in numbers of vertebrae, plicae, and dorsal and anal fin rays, particularly in the offshore *A. dubius*. Specimens from the Scotian Shelf north have higher counts than do specimens from more southern populations. Based on specimens examined, *A. americanus* occurs from southern Delaware north to Labrador in shallow coastal waters as well as in protected bays and estuaries. *Ammodytes dubius* is found in deeper, open waters from North Carolina to Greenland.

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Members of the genus *Ammodytes*, or sand lances, are small elongate fishes abundant over shallow, sandy areas of the continental shelves of northern oceans. They are important prey items for several commercial fishes (e.g., American plaice, cod, haddock, silver hake, yellowtail flounder, and Atlantic salmon (Reay 1970, Meyer et al. 1979, Winters 1983) as well as fin and humpback whales (Overholtz and Nicolas 1979) and various kinds of seabirds (Reay 1970, Powers and Backus 1987). Additionally, in the North Sea and off Japan, sand lances are the basis for an important fish-meal industry (Macer 1966).

Western North Atlantic populations of sand lances have increased dramatically in recent years (Sherman et al. 1981, Winters 1983). This population explosion was correlated with a decline in stocks of herring *Clupea harengus* and mackerel *Scomber scombrus* along the eastern coast of the United States (Population Dynamics Branch, Conservation and Utilization Div., Northeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA 02543) (Fig. 1). The opportunistic sand lances seemed to have replaced these stocks. Concurrently, piscivorous fishes increased their consumption of sand lances. Peak abundance of sand lances in this region was reached in 1981, and numbers have since decreased (Nelson and Ross 1987). Again, the shift in sand lance abundance was correlated with mackerel numbers; mackerel populations have been steadily increasing since 1983 (Fig. 1). In view of the ecological importance and population dynamics of sand lances, it is important that the taxonomic status of these fishes be resolved.

Although the taxonomy of the majority of fish species in the western North Atlantic Ocean is known reasonably well, *Ammodytes* is a major exception despite the results of several detailed studies (e.g., Richards et al. 1963, Scott 1972, Winters and Dalley 1988). Recognition of two species of *Ammodytes* in the western North Atlantic dates back to at least Jordan and Evermann (1896). Since then, the majority of researchers have fundamentally accepted this finding (Bruun 1941, Backus 1957, Richards et al. 1963, Leim and Scott 1966, Winters 1970, Scott 1972, Winters and Dalley 1988, Scott and Scott 1988). However, final conclusions on species names, synonomies, and meristic and geographic ranges vary between studies. *Ammodytes americanus* DeKay 1842 and *A. dubius* Reinhardt 1838 are currently accepted as the appropriate names for these sand lances (Leim and Scott 1966, Reay 1970, Richards 1982, Winters and Dalley 1988), and until a worldwide systematic revision

of the family is completed these names should be used.

Taxonomic confusion results mainly from the morphological similarity and large variability in characters traditionally used to separate and identify the different species of *Ammodytes*. Generally, distinguishing characters have been limited to meristic ones, especially numbers of vertebrae and dorsal and anal fin rays. Meristic overlap and variability are further complicated by the trend for more northerly populations of both species to have higher counts. Meristic characters show clinal variation, increasing both with latitude and distance offshore (Richards et al. 1963, Scott 1972, Richards 1982). Body depth and maximum total length have also been used to separate species (Richards et al. 1963, Winters and Dalley 1988), although this character combination has been shown to vary greatly with stage of maturity and age. In fact, intraspecific variation is greater than interspecific variation in some cases (Scott 1972). Additionally, the phase of the reproductive cycle and the amount of food present in the digestive tract also affect body depth in these fish.

With numerous hypotheses and species names circulating in the literature (see Richards et al. 1963 and Winters and Dalley 1988 for additional reviews), a need to alleviate some of the confusion associated with this genus is obvious. The western North Atlantic sand lances were studied in detail to determine appropriate species definitions, delimit geographic distributions, and describe meristic variation.

Historical background

Systematic problems involving *Ammodytes* are prevalent at all levels of taxonomic complexity. Researchers still are not sure of the phylogenetic relationships between genera of sand lances and the systematic placement of the Ammodytidae among perciforms. Pietsch and Zabetian (1990), however, believe ammodytids to be trachinoids with the family Ammodytidae the sister group of the Trachinidae plus Uranoscopidae.

At the alpha taxonomy level, 23 nominal species of the genus *Ammodytes* have been described. However, only the following six species have been consistently recognized in the literature: *A. americanus* DeKay 1842 and *A. dubius* Reinhardt 1838 in the western North Atlantic, *A. marinus* Raitt 1934 and *A. tobianus* Linnaeus 1758 in the eastern North Atlantic, and *A. hexapterus* Pallas 1811 and *A. personatus* Girard 1857 in the North Pacific (Reay 1970). However, Reay's (1970) synopsis of valid species names and delimitations of geographic ranges has not always been accepted; synonymies and geographical range adjustments are abundant. For instance, several workers including

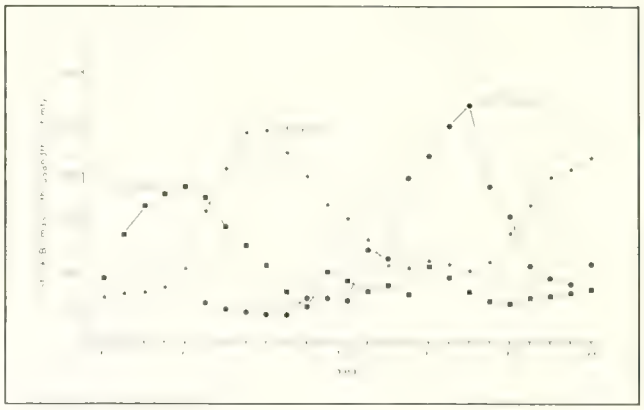

Figure 1

Abundance (10^6 metric tons) of mackerel *Scomber scombrus*, herring *Clupea harengus*, and sand lance *Ammodytes dubius* populations, 1963–87, in the western North Atlantic (Northeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA).

Andriashev (1954), Walters (1955), McAllister (1960), and Richards et al. (1963) have proposed that *A. hexapterus* is circumpolar and synonymous with *A. americanus* and/or *A. marinus*. Regarding the sand lances that occur in the extreme northern oceans (particularly Greenland), some investigators suggest that the low-count inshore form should be regarded as *A. americanus* (Reay 1970). Winters and Dalley (1988) proposed that these northern populations were *A. marinus*. Thus, these two nominal species may be conspecific, but researchers disagree on which name to use for the species in the western North Atlantic. *Ammodytes dubius* also occurs off the coast of Greenland but generally is considered to be a distinct species (e.g., Backus 1957, Reay 1970, Winters and Dalley 1988). Additionally, Jensen (1941, 1944) suggested that the broad overlap in characters used to separate *Ammodytes* species is so great that there may be only one extremely variable, polymorphic Atlantic species of sand lance.

Furthermore, clinal variation adds to the taxonomic confusion since some investigators recognize this variation as worthy of species designation while others propose the use of subspecies or only recognize isolated populations. Richards et al. (1963) suggested that clinal variation may be due to effects of environmental factors such as temperature, a phenomenon that has been documented in many other marine fishes. These trends have been reported in all species of *Ammodytes*, again leading to the suggestion of a single heterogeneous species with meristic and morphological differences attributable to environmental variables related to distribution.

Methods

Approximately 1500 specimens from a range of locations (North Carolina to Greenland) along the western North Atlantic coast were examined in this study (Fig. 2; Appendix 1). Total number of gill rakers were counted on the first arch on the right side; pectoral fin rays were counted on the left. Dorsal and anal ray counts were obtained from radiographs. The anterior 1–3 pterygiophores of the dorsal fin may have no associated fin ray; therefore, dorsal fin counts began at the first visible ray. Several cleared and stained specimens were examined to verify counts obtained from radiographs. Precaudal, caudal, and total vertebral counts were also taken from radiographs. The first caudal vertebra was defined as the centrum bearing the first elongate hemal spine. Total vertebral counts exclude the hypural plate following the practice of most recent workers on the genus.

Sand lances possess distinctive rows of oblique folds of skin or plicae which occur on the lateral body surfaces and are lined on the undersides by cycloid scales. The rows of plicae characteristically extend from an area above the pectoral fin base to the caudal peduncle. Plicae length and the angle of direction at which plicae run are highly variable near the head and tail (Fig. 3). Total plicae counts proved difficult to make and were not repeatable. Therefore, we modified plicae counts to begin with the first plica posterior to the first

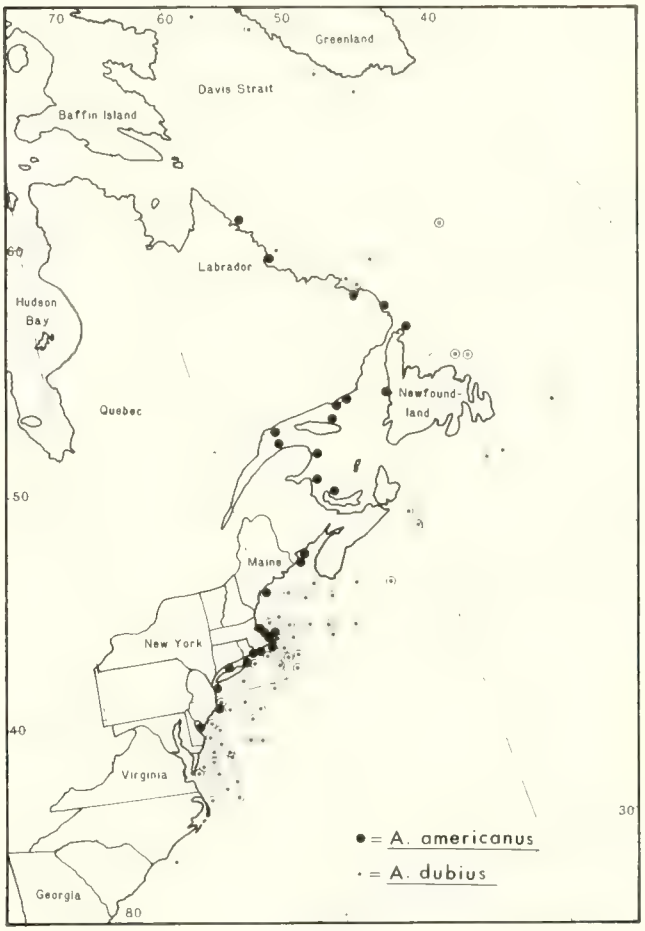

Figure 2

Distribution of *Ammodytes americanus* and *A. dubius* in western North Atlantic based on specimens examined for this study.

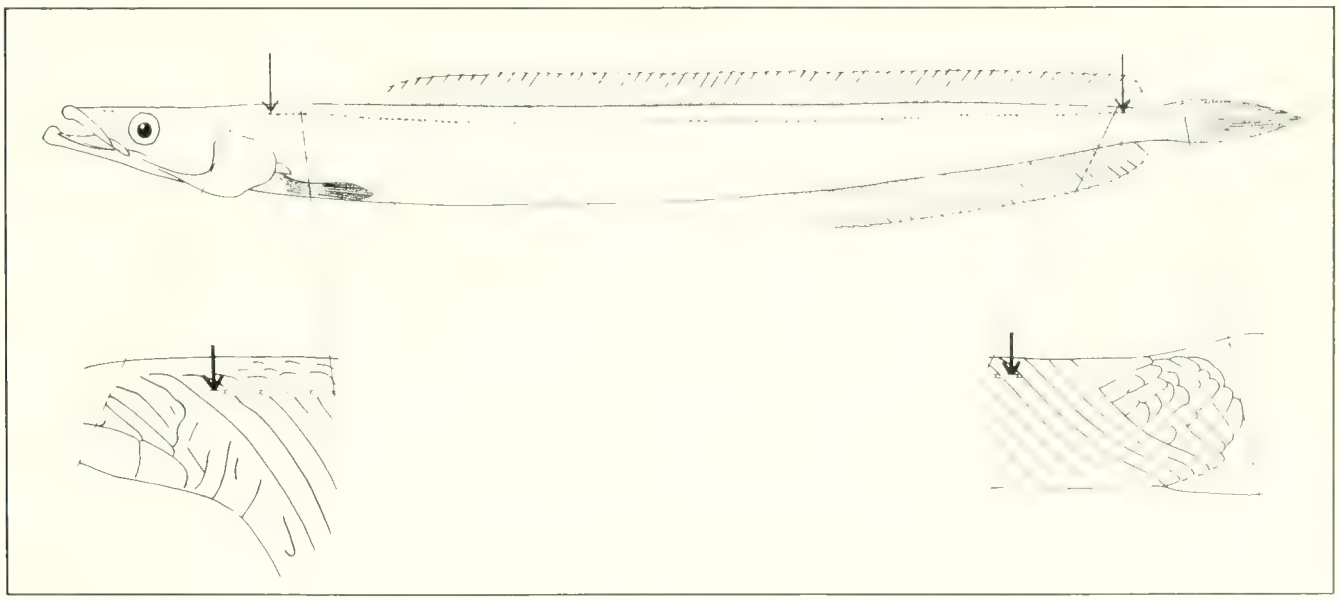

Figure 3

Drawing of *Ammodytes dubius* shows how plicae were counted (between arrows). The irregular plicae present anteriorly and posteriorly (see insets) were not counted.

pored lateral line scale and continuing posteriorly to the plica associated with the last pored scale (Fig. 3). Because plicae are much easier to count than scales, the folds themselves were counted between the two end points. If, however, the regular serial arrangement of plicae was interrupted (i.e., size and direction of slope of the plicae become irregular), the pored lateral line scales were counted in order to maintain consistency in counts between specimens. Plicae counts made in this manner are much more consistent.

Meristic data were divided into four geographic regions in order to describe and analyze geographic variation: Labrador, Quebec–Nova Scotia, Maine–Massachusetts, and New York–North Carolina. Since three species of *Ammodytes* may be present in Greenland waters, Greenland specimens were analyzed separately. Conclusions made with regard to the other geographic regions were applied to Greenland collections in an effort to determine which species are present in this region.

To determine if two species could be distinguished objectively, principle component analysis (PCA) was conducted on a covariance matrix for meristic characters (plicae, vertebrae, dorsal, anal, and pectoral fin rays, and gill rakers) for 332 individuals. These specimens, all with a complete complement of meristic values, were pooled from locations throughout the geographic range, exclusive of Greenland. An attempt was made to give equal representation to each area; however, there were not many offshore collections from Labrador available. Since the data set contained both individuals with low meristics and those with high counts, the assumption was made that both forms were present within the sample. An individual's score on the first component was determined by entering its values for meristic characters into an equation. Component scores were plotted and two groups are clearly present (Fig. 4). The point of least overlap was chosen as the boundary between the two species. Data points were then coded using earlier tentative identifications (based on observed meristic trends) to determine the effectiveness of the methodology. The equation and the value of the score at the boundary between the two species were cross-validated by testing an additional 54 specimens.

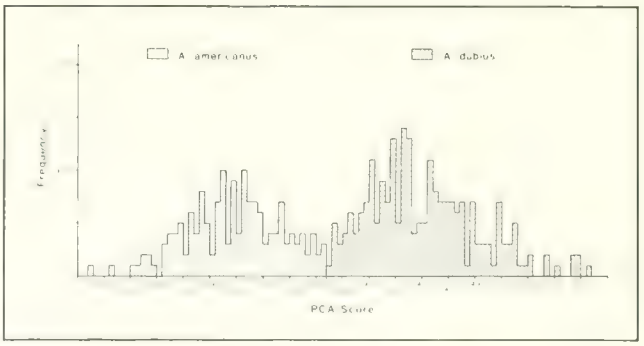

Figure 4

Histogram of principal component analysis (PCA) scores for six meristic characters of *Ammodytes*. Ranges: *A. americanus* 1199–1378, *A. dubius* 1378–1572. Component scores were calculated using the following equation: (8.09 × number of plicae) + (2.44 × number of dorsal rays) + (2.31 × total number of vertebrae) + (1.23 × total number of gill rakers) + (1.03 × number of anal rays) + (0.45 × number of pectoral rays).

Results

Number of lateral plicae was the most useful single character in separating the two species, even though plicae numbers varied considerably between individuals and slightly from side to side in individual specimens (Table 1). Of 723 specimens included in the analysis, 98.8% could be separated into species at a line of separation between 124 and 125 plicae (Fig. 5). *Ammodytes americanus* had fewer plicae, ranging from 106 to 126 ($\bar{x}$ 117.4) with virtually no geographic variation; *A. dubius* had more plicae (124–147, $\bar{x}$ 132.1) and exhibited geographic variation. Plicae means for *A. dubius* ranged from 131.2 in the New York–North Carolina region to approximately 132–136 from Massachusetts northward.

Number of vertebrae, a standard character examined by previous researchers interested in *Ammodytes*, also proved to be a relatively good character in separating species. Although some overlap in vertebral numbers exists, particularly south of Nova Scotia, 92.3% separation was achieved at a line of separation between 68 and 69 vertebrae (Table 2). *Ammodytes americanus* had fewer vertebrae, with mean values ranging from 65.2 in specimens from New York to North Carolina and increasing to a mean value of 67.2 in specimens from Quebec to Labrador. *Ammodytes dubius* characteristically had more vertebrae than *A. americanus*, with means ranging between 70–71 in the southern portions of its range (Maine to North Carolina) to 73.8 in the Quebec–Nova Scotia region and 71.9 off Labrador. There is a distinct increase in vertebral number ($\bar{x}$ 72.9) in specimens of *A. dubius* taken off the Scotian Shelf and northward.

Dorsal ray counts were also effective in separating specimens. Using this character alone, 92.3% of the specimens could be separated at a line of separation between 59 and 60 dorsal rays. *Ammodytes americanus* had relatively consistent dorsal ray counts throughout the entire geographic range (Table 3; 52–61, $\bar{x}$ 57.4); however, in comparison, number of dorsal rays for *A. dubius* was higher for specimens collected north of

Table 1

Frequency distribution of plicae counts for *Ammodytes americanus* and *A. dubius* in four geographic regions.

	A. americanus					*A. dubius*				
	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total
106			1		1					
107			1		1					
108	1		1		2					
109	1		–	1	2					
110	1	1	1	2	5					
111	2	5	–	1	8					
112	5	1	7	3	16					
113	2	2	1	8	13					
114	5	4	8	16	33					
115	7	4	7	7	25					
116	10	4	3	11	28					
117	10	7	8	10	35					
118	18	9	5	12	44					
119	13	2	6	6	27					
120	8	2	6	5	21					
121	8	9	6	5	28					
122	8	3	6	2	19					
123	1	2	4	7	14					
124	1	2	8	5	16	1		2	2	5
125	1			2	3	3	1	–	8	12
126	1				1	2	–	2	10	14
127						4	–	2	25	31
128						1	–	3	14	18
129						1	3	4	24	32
130						2	2	8	33	45
131						1	2	6	20	29
132						2	3	9	18	32
133						–	1	1	22	24
134						1	6	8	23	38
135						1	2	2	19	24
136						–	3	3	9	15
137						1	8	3	6	18
138						–	4	4	5	13
139						4	4	1	3	12
140						1	2	2	1	6
141						–	2	–	–	2
142						–	–	–	–	–
143						2	3		1	6
144							1	1	1	3
145							1	–		1
146								–		–
147								1		1
$\bar{x}$	117.6	117.4	117.7	116.1	117.4	131.8	136.0	132.6	131.2	132.1
N	103	57	79	103	342	27	48	62	244	381

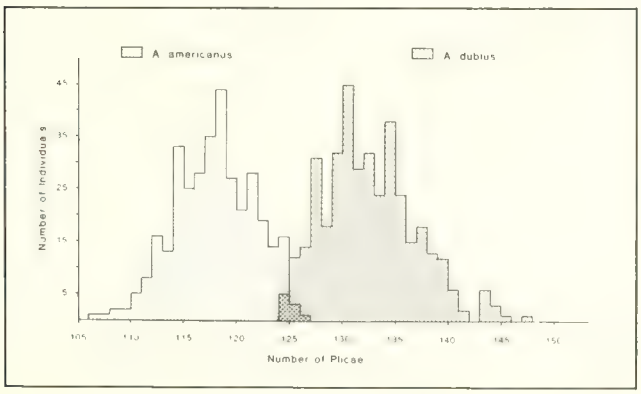

Figure 5

Histogram of counts of lateral plicae for *Ammodytes americanus* (106–126, $\bar{x}$ 117.4) and *A. dubius* (124–147, $\bar{x}$ 132.1).

Table 2

Frequency distribution of vertebral counts for *Ammodytes americanus* and *A. dubius* in four geographic regions.

	A. americanus					*A. dubius*				
	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total
62				2	2					
63	1			8	9					
64	6	1	11	18	36					
65	4	3	9	40	56					
66	17	8	14	16	55					
67	24	21	16	7	68					
68	29	16	18	3	66	2			16	18
69	15	4	7	4	30	3		12	39	54
70	1	1	2	1	5	5		23	87	115
71						3	1	22	64	90
72						2	3	3	23	31
73						2	15	1	4	22
74						6	14			20
75						4	8			12
76							3			3
$\bar{x}$	67.2	67.2	66.6	65.2	66.4	71.9	73.8	70.3	70.2	70.8
N	97	54	77	99	327	27	44	61	233	365

Table 3

Frequency distribution of dorsal ray counts for *Ammodytes americanus* and *A. dubius* in four geographic regions.

	A. americanus					*A. dubius*				
	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total
52			1		1					
53	1		2	1	4					
54	1	2	3	2	8					
55	1	4	5	7	17					
56	12	5	9	7	33				1	1
57	15	16	8	8	47				—	—
58	21	10	8	5	44	1		1	2	4
59	19	10	8	2	39	4		1	11	16
60	12		3	2	17	2		3	35	40
61	1		1	3	5	1		12	77	90
62						3	2	19	80	104
63						1	7	6	23	37
64						2	14		6	24
65						2	11			13
66						3	6			9
67						1	2			3
$\bar{x}$	57.9	57.2	56.9	56.9	57.4	62.4	64.4	61.5	61.3	61.8
N	83	47	48	37	215	20	42	42	235	341

Maine. Overall, dorsal ray counts for *A. dubius* varied from 56 to 67 rays. Specimens examined had means of 62.4 and 64.4 for Labrador and Quebec–Nova Scotia, respectively, compared with 61.5 in Maine–Massachusetts and 61.3 in the New York–North Carolina region.

Anal rays, the least successful character for separating specimens (Table 4), provided only 75.7% separation of individuals (at a line of separation between 29 and 30 anal rays). Means for *A. americanus* ranged from 29 in southern regions to 29.7 off the coast of Quebec northward to Labrador, with total number of rays varying between 26 and 33 (overall $\bar{x}$ 29.4). Geographic variation was again evident in anal ray counts for *A. dubius*. Counts averaged between 30 and 31 rays

Table 4

Frequency distribution of anal ray counts for *Ammodytes americanus* and *A. dubius* in four geographic regions.

	A. americanus					*A. dubius*				
	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total
26			2		2					
27	4	2	6	6	18					
28	10	4	15	3	32				4	4
29	23	13	8	15	59			1	27	28
30	27	18	8	9	62	2		17	76	95
31	13	9	7	4	33	6	2	15	99	122
32	6	2	3		11	6	6	11	32	55
33	1				1	4	17		5	26
34						3	14			17
35						1	7			8
$\bar{x}$	29.7	29.7	29.0	29.1	29.4	32.1	33.4	30.8	30.6	31.1
N	84	48	49	37	218	22	46	44	243	355

Table 5

Frequency distribution of pectoral ray counts for *Ammodytes americanus* and *A. dubius* in four geographic regions.

	A. americanus					*A. dubius*				
	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total
11			1		1					
12	12	5	14	10	41	1			4	5
13	62	40	49	53	204	17	2	10	35	64
14	20	11	14	35	80	6	25	39	155	255
15	1	1	1	5	8	3	21	14	47	85
16									2	2
$\bar{x}$	13.1	13.1	13.0	13.3	13.2	13.4	14.4	14.1	14.0	14.0
N	95	57	79	103	334	27	48	63	243	381

for specimens collected south of the Scotian Shelf (New York–North Carolina, $\bar{x}$ 30.6; Maine–Massachusetts, $\bar{x}$ 30.8) while specimens collected further north had mean values of 33.4 (Quebec–Nova Scotia) and 32.1 (Labrador).

The number of pectoral rays varied little geographically (Table 5) and was one of the least successful characters for separating the species. Modally, *A. americanus* had 13 rays (11–15, $\bar{x}$ 13.2) while *A. dubius* had one more ray, 14 (12–16, $\bar{x}$ 14.0). Only 78.0% of the specimens could be separated solely on this character (at a line of separation between 13 and 14 pectoral rays).

Gill rakers did not show pronounced geographic trends as was evident for vertebral counts (Table 6). For *A. americanus*, counts varied between 21 and 28, with means ranging from 23.7 (Labrador) to 24.9 (Massachusetts–Maine). Mean values for *A. dubius* clustered around 26 or 27 gill rakers ($\bar{x}$ 26.6, range 23–31 overall). At a line of separation between 25 and 26 gill rakers, 81.4% of the specimens could be separated into species using only this character.

Ammodytes dubius showed geographic variation in all the meristic characters examined. Meristic values increased northward with the exception of Labrador. Offshore Labrador collections were sparse; therefore, sample size is only half as large as other regions. Examination of additional material is necessary to determine if meristic values for *A. dubius* collected off Labrador are consistently lower.

The meristic characters used in this study separate the western North Atlantic sand lances into low- and high-count species. Each character, however, exhibited some overlap (ranging from approximately 3% for plicae counts to 49% for anal rays) and did not separate 100% of the specimens. Combinations of characters then became important in verifying identifications, particularly for individuals with intermediate counts.

Table 6

Frequency distribution of gill raker counts for *Ammodytes americanus* and *A. dubius* in four geographic regions.

	A. americanus					*A. dubius*				
	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total
21	1				1					
22	9	5	1		15					
23	30	18	7	13	68	4		1		5
24	28	22	19	29	98	5	1	4	7	17
25	18	7	23	22	70	4	3	8	37	52
26	2	5	14	15	36	1	9	18	70	101
27			5	5	10	4	10	7	66	87
28			1	1	2	2	13	6	50	71
29							7	–	9	16
30							1	1	3	5
31							2			2
$\bar{x}$	23.7	23.8	24.9	24.7	24.3	25.2	27.4	26.1	26.6	26.6
N	88	57	70	85	300	23	46	45	242	356

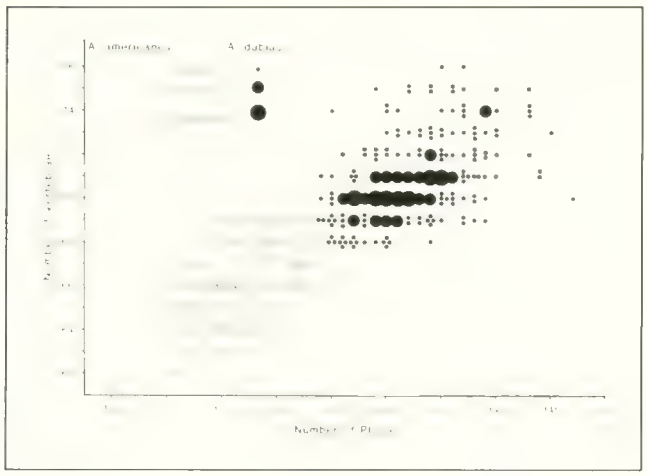

Figure 6

Scattergram of vertebral count plotted against number of lateral plicae for *Ammodytes americanus* and *A. dubius*.

Plicae and vertebral counts, when plotted against one another, were the most useful combination of characters for the entire geographic range producing virtually 100% separation (Fig. 6).

The results of a PCA run on meristic data confirmed the usefulness of these characters. Since factor 1 accounted for 91% of the variation and all the meristic characters loaded heavily on this factor, factor 1 was the only factor used. Plicae had the highest component loading score (8.09) followed by dorsal rays (2.44), vertebrae (2.31), gill rakers (1.23), anal rays (1.03), and pectoral rays (0.45).

The histogram of component scores (Fig. 4) produced a bimodal distribution with little overlap above or below a score of 1378 for the first set of individuals evaluated. When the scores were compared with the earlier tentative identifications (based only on meristics), only 10 (5 of each species) were either borderline or placed into the wrong species grouping. These 10 individuals were then reexamined and either the proposed identification was verified (3 cases) or errors in the counts of certain meristic characters were found (7 cases).

At most, 2% of the specimens were misclassified using the component scores. Of 54 additional specimens tested against the equation, none were misclassified. This methodology, therefore, was consistent and reliable.

Based on these results, diagnoses for the two species follow:

Ammodytes americanus

Diagnosis *Ammodytes americanus* tends to have lower counts than *A. dubius*: lateral plicae 106–126 ($\bar{x}$ 117.4); vertebrae 62–70, usually 64–69 ($\bar{x}$ 66.4); dorsal fin rays 52–61 ($\bar{x}$ 57.4), anal fin rays 26–33 ($\bar{x}$ 29.4), and pectoral fin rays 11–15 ($\bar{x}$ 13.2), with the most common dorsal, anal, and pectoral ray counts being 55–59, 27–31, and 13 rays, respectively; gill rakers on the first arch 21–28 ($\bar{x}$ 24.3).

Six meristic characters in combination provide a good separation of this species from *A. dubius*. Number of plicae, however, is the single best character for distinguishing *A. americanus* from *A. dubius* in the western North Atlantic. Vertebrae plotted against plicae separate individuals of the two species with little overlap (Fig. 6).

Distribution Based on our samples, *A. americanus* ranges coastally from southern Delaware north through

Labrador (Fig. 2). Previous studies reported its occurrence in Chesapeake Bay (Richards 1982, Norcross et al. 1961); however, no specimens were examined from Chesapeake Bay during this study.

This species occurs in shallow coastal waters and in protected bays and estuaries. Frequently, specimens were collected with seines or dipnets on sandy beaches in less than 2 m of water. Identification of individuals based only on locality (i.e., inshore vs. offshore) can be made with discretion, but some collections (approximately 20%), mainly from inshore stations, contain both species.

Ammodytes dubius

Diagnosis *Ammodytes dubius* shows geographic variation in meristic features (Tables 1–6), and counts for this species are higher than those of *A. americanus*: lateral plicae 124–147 ($\bar{x}$ 132.1); vertebrae 68–76 ($\bar{x}$ 70.8) with 69–74 being the most common; dorsal fin rays 56–67 ($\bar{x}$ 61.8), anal fin rays 28–35 ($\bar{x}$ 31.1), and pectoral fin rays 12–16 ($\bar{x}$ 14.0). The majority of individuals examined have ⩾60 dorsal, ⩾29 anal, and 14 pectoral rays. More gill rakers (23–31, $\bar{x}$ 26.6) are present on the first arch than in *A. americanus*. As described previously, plicae count is the best single distinguishing character; however, vertebrae plotted against plicae separate the species with little overlap (Fig. 6).

Distribution *Ammodytes dubius* ranges from North Carolina to Greenland (Fig. 2) and is found in deeper, more offshore waters than *A. americanus*. *Ammodytes dubius* is occasionally found inshore but is generally taken in deeper, open waters. This species has a broad bathymetric distribution in coastal waters and ranges in depth from 7 to 80 m. Both species were taken together in approximately 20% of the samples examined, with the majority of these samples being collected at inshore stations or around islands just offshore. Winters and Dalley (1988) reported co-occurrence inshore of *A. americanus* and *A. dubius*, particularly in Newfoundland waters. Although none of the collections that we examined from Quebec–Nova Scotia contained both species, mixed collections were found in all other geographic areas. Several mixed collections (6 of 11 collections) contained only one or two individuals of *A. dubius*, with the remainder of the lot being *A. americanus*. Two of the 11 collections were all *A. dubius* except for one specimen of *A. americanus*.

Greenland *Ammodytes* Since doubts exist with regard to the number of species and the appropriate names of species occurring in Greenland, these specimens were analyzed separately using the PCA equation and diagnoses used in analyzing and describing the species in other regions. Only those specimens (N = 51) with complete meristic data were included in the analysis. The majority of specimens fit our definition of *A. dubius*. Vertebral counts ranged from 66 to 75 ($\bar{x}$ 70.8); plicae counts from 124 to 156 ($\bar{x}$ 133.4); PCA scores from 1388 to 1636. Two specimens, however, fit our definition of *A. americanus*; one specimen had 70 vertebrae, 123 plicae, and a PCA score of 1374, and the other had 68 vertebrae, 124 plicae, and a score of 1372.

Discussion

Results of this study demonstrate, in accordance with the majority of previous research (Richards et al. 1963, Leim and Scott 1966, Winters 1970, Scott 1972, Richards 1982), that two species of sand lances occur in the western North Atlantic: an inshore species, *A. americanus*, with low meristic features, and an offshore species, *A. dubius*, characterized by high meristics.

No unequivocal method has been demonstrated previously to consistently identify individuals of *A. americanus* and *A. dubius*. Counts purportedly delineating the two species varied between studies, and considerable variation in meristic features for either one or both of these species has been reported. Additionally, earlier studies relied principally on vertebral counts (with supporting data from dorsal and anal ray counts) but this approach was inadequate to accurately identify all individuals. Plicae count, the most useful character in our study, was not used in the majority of previous studies. Furthermore, the lack of published detailed locality data in the majority of previous studies, consistent inshore/offshore designations, and a full understanding of migration patterns (Reay 1970) have added to the confusion in taxonomic status and ability to accurately identify species.

With no clear-cut definition of the western North Atlantic species, identification problems have hindered previous investigators. A case in point is the reported discrepancy in geographic distribution of *A. dubius* and resultant interpretations of species. Since the earliest studies by Reinhardt (1838) and DeKay (1842), species designations have not been consistent. Reinhardt (1838) described *A. dubius* from Greenland. Jordan and Evermann (1896) later reported that this species occasionally reached as far south as Cape Cod. In the revision of the Ammodytidae by Duncker and Mohr (1939), *A. dubius* was reported from throughout the North Atlantic. However, the majority of recent researchers disagree and have limited the range of *A. dubius* to the western North Atlantic. In 1963, Richards et al. reported *A. dubius* as extending

further south to Virginia (37°N). Later Richards (1982), for no stated reason, reported a more limited distribution for *A. dubius*, with no individuals found further south than the Scotian Shelf. Winters and Dalley (1988) also reported *A. dubius* as ranging no further south than Georges Bank.

Restricting the southern limit of the range for *A. dubius* to Georges Bank creates several problems, in particular the explanation of a southern offshore, high-meristic form. Richards et al. (1963), Richards (1982), and Winters and Dalley (1988) recognized two populations of *A. americanus* in southern waters: one an inshore low-meristic form, and the other an offshore, intermediate- to high-meristic form. This conclusion seems to stem from Perlmutter's (1940) recognition of two offshore populations, one occurring north and one south of Cape Cod, which were designated as subspecies of *A. tobianus*. In those studies (Richards et al. 1963, Richards 1982, Winters and Dalley 1988), *A. americanus* was probably chosen for the species name for southern offshore specimens because meristic values (vertebrae, dorsal and anal fin rays) were more similar to the counts they found for *A. americanus* than for northern *A. dubius*. However, all of these studies reported and accepted the existence of a north-south and/or an inshore-offshore cline for at least one (but not always the same) species. Furthermore, the offshore *A. americanus* occupied the habitat commonly inhabited by *A. dubius*. Also, the morphometric description given by Winters and Dalley (1988) for their southern offshore *A. americanus* was the same as that for their *A. dubius*. Meristic differences between inshore and offshore *Ammodytes* in southern waters are consistent with a hypothesis of two distinct sympatric—but not necessarily syntopic—species, *A. americanus* and *A. dubius*, occurring in these waters. Additionally, meristic variation between northern and southern offshore forms supports the hypothesis of geographic intraspecific variation for *A. dubius*. The data are not consistent with a hypothesis recognizing only *A. americanus* in the southern region.

Misconceptions regarding species designations of western North Atlantic *Ammodytes* are further compounded by the tendency of some authors (Richards et al. 1963, Winters and Dalley 1988) to create three groups—a low, intermediate, and high meristic group—within their data sets to explain the variation, instead of recognizing geographic variation in the offshore species. Recognizing three groups results in considerable overlap between groups, thus adding to the difficulty of identifying species. Modal analysis (only for vertebrae; Winters and Dalley 1988) in some cases seems to identify modes that are not immediately obvious in the accompanying figures or data. The accuracy of identifying groups within collections, let alone individuals, is questionable using this method. The number of components and first estimates of the modes and standard deviation must be specified first. Additionally, as Winters and Dalley (1988) point out, the reported high standard error for certain modes indicates that these means are estimated poorly.

To eliminate confusion or guesswork surrounding identification of individuals of *Ammodytes*, it was necessary to devise an objective method of identification. PCA achieves this goal since this method identifies patterns of variation between individuals without regard to the groups represented. PCA scores were utilized as a tool to summarize the data and to verify the usefulness of these meristic characters. A plot of the component scores of 332 individuals clearly showed two groups (Fig. 4). Further testing showed that these groups represent the two species. Thus, the two species can be separated using meristic characters instead of morphometric ratios of questionable validity (i.e., length-weight; see Scott 1972) with little overlap.

Furthermore, by designating a component score boundary between the two groups, the two species are clearly defined and meristic variation can be delimited for each of the two species. This is particularly important for individuals with intermediate counts, especially those occurring in collections containing both species. These individuals were the hardest to identify, but defined limits for plicae, vertebral, and dorsal ray counts made identifications easier.

To support our data analysis, a comparison with Perlmutter's 1940 data was made (Table 7; in the present study, Northern = Labrador and Quebec–Nova Scotia, Southern = Maine–Massachusetts and New York–North Carolina). The Perlmutter (1940) data were utilized because the data collected and geographic locations were similar. Designations of north-south as well as inshore-offshore locations were given also. Means for meristic data were surprisingly similar between the two studies.

Perlmutter (1940) recognized north-south and inshore-offshore clines in his data, yet misinterpreted these results. He designated several subspecies within a single worldwide polytypic form instead of recognizing geographic variation within two parapatric species. Evidence for recognition of two species is that both species have been collected in sympatry in coastal waters, particularly in the Newfoundland area. It has been postulated that *A. dubius* spawns inshore along the Newfoundland coast (Dalley and Winters 1987). The continued occurrence of high meristic individuals inshore suggests that these species are reproductively isolated (Winters and Dalley 1988). Our data provide additional support for recognition of two parapatric species since there tend to be ecological differences between the species, in particular, habitat preference.

Table 7
Comparison of mean meristic values for characters used by Perlmutter (1940) and in the present study.

	Perlmutter (1940) $\bar{x}$	Nizinski et al.[1] $\bar{x}$
Vertebrae[2]		
A. americanus		
Northern	67.3	67.0
Southern	65.5	65.2
A. dubius		
Northern	73.5	72.0
Southern	70.0	70.2
Dorsal rays		
A. americanus		
Northern	57.0	57.3
Southern	55.3	56.9
A. dubius		
Northern	63.3	62.8
Southern	60.3	61.3
Anal rays		
A. americanus		
Northern	28.8	29.5
Southern	27.6	29.1
A. dubius		
Northern	32.3	32.1
Southern	29.6	30.6
Pectoral rays		
A. americanus		
Northern	13.2	13.1
Southern	13.7	13.3
A. dubius		
Northern	14.4	14.0
Southern	14.2	14.0

[1]Northern = Labrador and Quebec–Nova Scotia
Southern = Maine–Massachusetts and New York–North Carolina
[2]Hypural plate excluded.

The majority of individuals have been collected either inshore (*A. americanus*) or offshore (*A. dubius*) with little syntopic occurrence. We conclude, therefore, that two distinct species, *A. americanus* and *A. dubius*, occur in the western North Atlantic Ocean.

A similar case has been reported for the species of *Ammodytes* (*A. personatus* and *A. hexapterus*) found off Japan. Populations of morphologically and meristically similar individuals are difficult to distinguish from one another. Electrophoretic data, however, suggest that two sympatric, genetically distinct groups do occur among these *Ammodytes* species (Okamoto 1989). Perhaps a similar analysis is needed for the western North Atlantic ammodytids to confirm species designations.

As previously mentioned, this study is a preliminary step toward understanding a more complex problem. Many other questions, including the taxonomic status of Greenland *Ammodytes*, remain unanswered. Specimens examined in our study ($N = 51$) had high counts, similar to those obtained for *A. dubius*. But counts for these individuals were highly variable and did not agree completely with those of *A. dubius* from the western North Atlantic. In particular, some specimens had low vertebral counts and extremely high plicae counts. Others with low plicae counts, albeit still in the range for *A. dubius*, tended to have high vertebral counts. Based on meristic combinations and computed PCA scores, the Greenland sand lance is most similar to *A. dubius*. This finding adds to the existing conflict over which species are found in Greenland. Published accounts indicate two species of sand lances occur in this region: high-meristic *A. dubius*, and a low-meristic, inshore species that has been called *A. marinus* by Winters and Dalley (1988) as were all western Atlantic *A. americanus*. However, there is some question to the identity of the low-meristic sand lance occurring in Greenland. Counts for these specimens match those of *A. americanus* as well as the European *A. marinus*. The low-meristic Greenland species has reportedly been dipnetted and seined on shallow beaches and in protected fjords. *Ammodytes marinus*, on the other hand, is described as the commonly occurring offshore, deeper-water species in the eastern North Atlantic (Richards et al. 1963, Wheeler 1969, Reay 1970), although this species has also been reported from inshore stations (Raitt 1934, Kirillov 1936).

A limited number of *A. marinus* from the British Isles were examined; however, the data from these fish posed more questions than solved existing problems. Meristic features of these specimens spanned the ranges recorded for *A. americanus/dubius*, and morphological differences between these three species were not distinctive. The problem is further complicated since *A. dubius* and *A. marinus* are believed to be on opposite shores of the Atlantic (Reay 1970) yet both have been reported from Greenland. The taxonomic status of *Ammodytes* occurring in Greenland waters cannot be resolved until meristic and geographic ranges of European *A. marinus* are determined.

Taxonomic confusion is not restricted to Atlantic species; the taxonomy of North Pacific *Ammodytes* is problematical as well. Researchers agree that *A. hexapterus* and *A. personatus* occur in Japanese waters (Kitaguchi 1979, Hashimoto 1984), with *A. hexapterus* reported as the more northern species and *A. personatus* as the more southerly species. But these species also are similar morphologically and have overlapping counts (vertebrae and dorsal and anal fin rays). Additionally, high variability with two existing modes in the meristic data suggest the presence of two subpopulations in the southern *A. personatus* group (Hashimoto

and Kawasaki 1981, Hashimoto 1984). Isozyme differences have indicated three separate genetic stocks (one *A. hexapterus* and two *A. personatus*; Hashimoto 1984), and recent electrophoretic analysis confirms the existence of a northern and southern population of *A. personatus* as well as a possible new species or subspecies (Okamota et al. 1988, Okamota 1989). Morphological differences, however, are not significant between populations and between species, and it remains to be decided if designation of subspecies within this species complex is appropriate (Hashimoto 1984).

Problems also occur in defining limits between North Pacific and western North Atlantic species of *Ammodytes*. Some investigators (Lindberg 1937, Andriashev 1954, Walters 1955, Richards et al. 1963) have suggested that *A. hexapterus* is circumpolar and extends from the Pacific into the Arctic and North Atlantic oceans. These workers have argued that *A. hexapterus* is synonymous with *A. americanus* and/or *A. marinus*. A limited number of *A. hexapterus* ($N = 5$) from Alaska and *A. marinus* ($N = 15$) from the British Isles were examined and no distinct morphological or meristic characters were found to clearly separate these species from those occurring in the western North Atlantic. Both *A. hexapterus* and *A. marinus*, however, are usually characterized as occurring in deeper, offshore waters. Obviously, the entire genus is in need of revision.

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Appendix 1: Material examined

Abbreviations of institutions

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia
ARC	Atlantic Reference Centre, Huntsman Marine Laboratory, St. Andrews, New Brunswick
FMNH	Field Museum of Natural History, Chicago
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
NMC	National Museum of Natural Science, Ottawa, Canada
UMMZ	University of Michigan Museum of Zoology, Ann Arbor, MI
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC
VIMS	Virginia Institute of Marine Science, Gloucester Point, VA
ZMUC	Kobenhavns Universitet Zoologisk Museum, Copenhagen, Denmark

Material is listed by species, geographically from north to south.

Ammodytes americanus

Labrador 177 specimens (49–157 mm SL) from nine collections. FMNH 31106–31116, 31118–31132 (25, 49–126) Anatalak Bay, Nain, Labrador; July–Aug. 1928. MCZ 12471 (8, 98–143) Labrador. MCZ 12480 (52, 80–145) Labrador. MCZ 12481 (17, 105–157) Labrador; Packard; 1865. MCZ 12482 (30, 85–155) Labrador. MCZ 51802 (4, 69–76) Hamilton Inlet, Collingham's Cove; *Blue Dolphin*; 7 Feb. 1952. USNM 165262 (1, 96) Indian Cove, Assyis Run, St. Lewis Sound, 52°15′N 55°04′W; *Blue Dolphin*; 12 July 1949. USNM 165300 (35, 96–147) Labrador, Hare Harbor, 53°43′N 56°46′W; *Blue*

Dolphin; 2 July 1950. USNM 165371 (5, 92–104) Labrador, mouth of Tessiujarsuk near Nain; *Blue Dolphin*; 8 Aug. 1951.

Newfoundland, Nova Scotia, and Quebec 90 specimens (52–147 mm SL) from 11 collections. MCZ 49725 (1, 147) Newfoundland, Nolan's Beach, Sweet Bay, Bonavista Bay; R.H. Backus; 7 June 1948. NMC 73-380 (3, 121–140) Newfoundland; Bonne Bay at Norris Point Wharf; B.E. Bowen; 9 July 1973. NMC 66-174 (1, 80) North Newfoundland, Griguet Harbor at Griguet, 51°32.5′N 55°28.5′W; D.E. McAllister and W.H. Vliet; 0–1 m; 18 June 1966. NMC 59-266 (38, 96–140) Quebec, Perce on tip of Gaspe Peninsula, Gaspe Co. 48°30′N 64°15′W; D.E. and N.A. McAllister; 0–1 m; 10 June 1959. NMC 81-0888 (11, 76–101) Quebec, Fleuve St. Laurent, 49°35′N 67°25′W; J.D. Dutil and B. Legare; 24 June 1981. USNM 88849 (1, 131) Quebec, north side of Matamer River; Amory-Bowman Expedition; 1927. ARC 8600807 (12, 97–124) Tabusintac estuary (gulley); M.J. Dadswell and G. Melvin; 0–1 m; 20 July 1977. ARC 8600809 (1, 90) New Brunswick; New River Beach; M.J. Dadswell et. al.; intertidal; 16 Sept. 1977. ARC 8600803 (1, 114) New Brunswick, St. Andrews; Oct 1949. UMMZ 193387 (20, 52–63) New Brunswick, Miramichi, inside West End Bay du Vin Island; R.A. McKenzie; 22 July 1942. ARC 8600802 (1, 125) Prince Edward Island; Aug. 1953.

Maine and Massachusetts 285 specimens (60–168 mm SL) from 14 collections. FMNH 17181–17185 (5, 141–168) Boothbay Harbor, ME; July 1931. MCZ 44877 (2, 95–102) MA, Barnstable Harbor; J. Morin. MCZ 57161 (14, 60–121) Chatham, upper Cockle Cove off Mill Creek Rd.; K.E. Hartel. MCZ 12464 (15, 86–123) Yarmouth; L. Agassiz. UMMZ 140537 (15, 106–133) MA, beach near Scituate between second cliff and third cliff; C.L. and L.C. Hubbs; 0–3 ft; 17 June 1928. USNM 302255 (126+, 75–105) Nahant, East Point, Marine Science Institute; B.B. Collette, BBC 1759; 0–1 m; 7 Aug. 1981. USNM 302256 (11, 76–108) 41°18′N 70°28′W; *Gloria Michelle* Cr. 8592, Sta. 57; 12 Sept. 1985. USNM 83720 (15, 91–128) MA, Truro; W.C. Kendall; 14 Sept. 1892. USNM 36925 (20, 101–119) MA, Bass Rocks, New Gloucester; A.H. Clark; Oct. 1879. USNM 132092 (20, 73–115) ME, Wood Island; *Grampus*; surface; 13 Oct. 1915. USNM 73499 (3, 97–105) MA, "The Cut" and Pavillion Beach, Gloucester; *Grampus*; 29 July 1895. USNM 302254 (10, 79–112) Newberry Port, MA, Merrimack R. USNM 302253 (22, 73–122) Martha's Vineyard Sound, MA. Fahay collection (7, 80–130) Nauset Marsh, Cape Cod; Fahay and Able.

New York to Virginia 199 specimens (83–137 mm SL) from three collections. AMNH 36590 (72, 89–120) NY, Suffolk Co., Sunken Meadows' State Park, east of Jetty Seine; G.J. Nelson et al.; 19 May 1977. AMNH 37692 (30, 83–118) Suffolk Co., Gardener's Island, tidal outlet, Bostwick's Pond; D.E. Rosen et al.; 22 Apr. 1977. ANSP 165786 (97, 83–137) approx. 2.5 naut. mi. SE of Little Egg Inlet, along axis of lump-5252; C.B. Milstein, CBM 72–145.

Ammodytes dubius

Labrador 14 specimens (121–203 mm SL) from two collections. USNM 165263 (11, 121–187) Pack's Harbor, 53°54′N 56°59′W; *Blue Dolphin*; 24 July 1949. USNM 165264 (3, 143–203) Hare Harbor; *Blue Dolphin*; 2 July 1950.

Newfoundland, Nova Scotia, and Quebec 72 specimens (107–244 mm SL) from five collections. NMC 64-763 (16, 178–209) off Newfoundland, Grand Banks, 45°06′30″N 49°01′00″W; *A.T. Cameron*; 14 Oct. 1964. NMC 64-764 (11, 169–244) off Newfoundland, Grand Banks, 54°02′50″N 49°04′15″W; *A.T. Cameron*; 5 Oct. 1964. VIMS 1224 (30, 192–230) 44°05′05″N 60°04′30″W; *A.T. Cameron* Cr. 176, Sta. 16. UMMZ 201715 (14, 107–195) Nova Scotia, caught on Middle Bank of Atlantic Ocean, 44°35′N 60°25′W; *S.T. Venosta*; Nov. 1938. ARC 8600808 (1, 155) Grand Bank, SE shoal water; G. Somerville; 8 July 1954.

Maine and Massachusetts 264 specimens (77–253 mm SL) from 15 collections. MCZ 40699 (1, 177) N. end Stellwagen Bank; F. Buinett. MCZ 62955 (3, 77–102) Martha's Vineyard, just off south coast between Chilmark and Edgartown; *Gloria Michelle* Cr. 8592, Sta. 53–56. VIMS 2293 (2, 249–253) 42°36′N 66°17′W; *Albatross IV* Cr. 6911, Sta. 214. USNM 67636 (4, 83–98) MA, North Truro, Cape Cod; *Grampus*; 9 June 1896. USNM 163734 (1, 256) Georges Bank, 41°21′N 67°33′W; R.L. Wigley; 1950. USNM 302242 (6, 80–128) 40°59′N 69°(26–28)′W; *Delaware II* Cr. 8207, Sta. 91; 44 m; 13 Oct. 1982. USNM 302245 (3, 112–122) 40°49′N 69°04′W – 40°48′N 69°05′W; *Delaware II* Cr. 8207, Sta. 92; 69 m; 14 Oct. 1982. USNM 302247 (15, 98–123) 41°21′N 67°26′W; *Delaware II* Cr. 8207, Sta. 123; 38 m; 21 Oct. 1982. USNM 302258 (55, 87–125) 41°28′N 67°46′W; *Delaware II* Cr. 8207, Sta. 124; 40 m; 21 Oct. 1982. USNM 302250 (26, 86–142) 41°33′N 67°58′W; *Delaware II* Cr. 8207, Sta. 125; 30 m; 21 Oct. 1982. USNM 302240 (17, 96–140) 41°38′N 68°27′W; *Delaware II* Cr. 8207, Sta. 128; 60 m; 22 Oct. 1982. USNM 302249 (10, 87–128) 41°35′N 66°58′W; *Delaware II* Cr. 8207, Sta. 143; 58 m; 23 Oct. 1982. USNM 302248 (50, 121–175) 41°51′N 70°29′W; *Gloria Michelle* Cr. 8592, Sta. 3; 13 m; 6 May 1986. USNM 302246 (45, 59–184) 41°35′N 69°56′W; *Gloria Michelle* Cr. 8592, Sta. 77; 7 m; 18 May 1986. USNM 302251 (46, 100–161) 42°05′N 70°08′W; *Gloria Michelle* Cr. 8592, Sta. 91; 16 m; 18 Sept. 1985. USNM 302257 (17, 84–108) 41°18′N 70°28′W; *Gloria Michelle* Cr. 8592, Sta. 57; 12 Sept. 1985.

New York to North Carolina 415 specimens (54–249 mm SL) from 24 collections. ANSP 36662-73 (13, 146–207) NJ, Carson's Inlet, Cape May Co.; R.J. Phillips; 1 Nov. 1908. VIMS 2294 (3, 175–193) 41°2.5′N 69°00′W; *Albatross IV* Cr. 7002. VIMS 2295 (19, 194–249) 39°03′N 73°41′W; *Albatross IV* Cr. 6908, Sta. 161. VIMS 2390 (1, 217) 28°28′N 74°37′W; *Sea Breeze*, Sta. T350. VIMS 2807 (3, 98–109) 37°51′N 75°08′W; McEachran. VIMS 2808 (9, 140–178) 38°07′N, 74°44′W; *Albatross IV* Cr. 6920, Sta. 2. VIMS 7377 (1, 186) 37°01′N 74°57′W, Virginia Shelf; *Captain Wool*. VIMS 7751 (4, 120–190) 40°47′N 69°40′W; *Albatross IV* Cr. 8005, Sta. 36, ANSP 165785 (153, 92–138) approx. 2.5 naut. mi. SE of Little Egg Inlet, along axis of lump-5252; C.B. Milstein, CBM 72–145. UMMZ 212624 (50, 100–185) NY, Plum Beach, Long Island; A. Perlmutter; 20 Dec. 1937. USNM 302243 (1, 159) 40°00′N 73°47′W – 40°01′N 73°44′W; *Delaware II* Cr. 8207, Sta. 44; 29 m; 8 Oct. 1982. USNM 302244 (3, 119–143) 41°11′N 71°24′W – 41°13′N 71°24′W; *Delaware II* Cr. 8207, Sta. 75; 38 m; 11 Oct. 1982. USNM 302241 (46, 54–182) 41°40′N 69°54′W; *Gloria Michelle* Cr. 8592, Sta. 78; 12 m; 19 May 1986. USNM 302229 (1, 132) 38°52′N 74°48′W; *Albatross IV* Cr. 8809, Sta. 78; 6.6 fm; 22 Sept. 1988. USNM 302230 (1, 117) 40°50′N 72°(22–24)′W; *Albatross IV* Cr. 8809, Sta. 135; 18 m; 27 Sept. 1988. USNM 302231 (1, 117) 36°55′N 75°52′W; *Albatross IV* Cr. 8809, Sta. 60; 5.7 fm; 19 Sept. 1988. USNM 302232 (15, 144–171) 39°24′N 73°29′W – 39°25′N 73°26′W; *Albatross IV* Cr. 8809, Sta. 95; 38 m; 23 Sept. 1988. USNM 302233 (25, 117–146) 38°47′N 74°08′W – 38°49′N 74°09′W; *Albatross IV* Cr. 8809, Sta. 84; 44 m; 22 Sept. 1988. USNM 302234 (1, 132) 40°40′N 72°58′W – 40°41′N 72°56′W; *Albatross IV* Cr. 8809, Sta. 130; 15 m; 26 Sept. 1988. USNM 302235 (20, 144–171) 39°23′N 73°43′W – 39°24′N 73°42′W; *Albatross IV* Cr. 8809, Sta. 94; 32 m; 23 Sept. 1988. USNM 302236 (2, 121–122) 37°(04–06)′N 75°18′W; *Albatross IV* Cr. 8809, Sta. 56; 27 m; 18 Sept. 1988. USNM 302237 (1, 125) 39°19′N 74°(21–23)′W; *Albatross IV* Cr. 8809, Sta. 88; 10 m; 22 Sept. 1988. USNM 302238 (24, 100–138) 36°46′N 75°24′W – 36°47′N 75°22′W; *Albatross IV* Cr. 8809, Sta. 54; 23 m; 18 Sept. 1988. USNM 302239 (18, 104–189)

38°47′N 73°15′W – 38°48′N 73°13′W; *Albatross IV* Cr. 8809, Sta. 3; 80 m; 13 Sept. 1988.

Ammodytes sp.

Greenland 55 specimens (48–192 mm). USNM 87373 (5, 48–55) P.H. Sorenson. MCZ 63338 (4, 63–77) 64°47.3′N 30°37.4′W; *Endevor* Cr. 133, Sta. 5. MCZ 63339 (2, 55–59) 65°23′N 29°22.8′W; *Endevor* Cr. 133, Sta. 12. ZMUC various lots (44, 57–192): 61150; store Hellefiskebanke, 24 Hum v.s.v. f. Rifkol, smaa sten; 10 July 1912; *Beskytteren*. P61152. P61153. P61154. P61158; Godhavn; Porsild. P61159; Bunden af. Kapisigdlitfjord øf lak seelven Aalehaandvaad; *Dana*, Sta. 2325. P61166; Greenland 66°44′N 53°W; *Dana*, Sta. 2349. P61312; Prøvens Havn, NV Grønland; Finn Salomonsen. P61322. P61324. 73; Grønland. 76. 78. 79. 84; 23/2, 49; N. 101. 89; Grønland. 9Od. 67°53′N 54°02′W. 121. 160; Jakobshavn; P. Müller. 161; Jakobshavn; P. Müller. 162; Claushavn; Ad. Jensen. 163; Disko Bügten. 165; Marrak i Sydostbugten, Opskyllet i Beg. af., Aug. 1906; Ad. Jensen. 169; Tkamiut i Sydostbugten; Lohmann. 170; Godhavn; Porsild. 176; Sukkertoppen; Bistrup. 178; Sukkertoppen; Bistrup. 179; Sukkertoppen; Bistrup. 180; Sukkertoppen; Bistrup. Uncat (15 spec.); Kigdluf Iluat, Grønland, 63°53′N 51°22′W.

Ammodytes marinus

USNM 302259 (2, 115–126) Brunswick Wharf; Thames and Wheeler. USNM 302260 (8, 88–148) Littlebrook and W. Thurrock; Thames. USNM 108812 (5, 160–171) British Isles; Firth of Forth, 56°12′N 2°43′W.

A. hexapterus

USNM 207553 (1, 159) AK, Cook Inlet, N. Barren Islands, S of Kenai Peninsula, 59°09′N 152°17′W; *Yaquina*; 60 fm; 30 July 1963. USNM 235313 (2, 91–143) AK, Aleutian Islands, NE Adak Island, southside of Clam Lagoon; J. Rosewater and P.R. Greenhall; 8 June 1979. USNM 266655 (2, 123–129) AK; *Miller Freeman*, Sta. B44; 14 Aug. 1982.

Abstract.– We computed correlations between various population estimates for Central California chinook salmon *Oncorhynchus tshawytscha* and both freshwater and marine environmental variables using methods that account for intraseries correlation in a more accurate and conservative way than those used previously. These indicated a negative influence of ENSO (El Niño-Southern Oscillation) conditions in the year during which most of these fish are caught or leave the ocean to spawn. Although freshwater environmental influences have been previously proposed on the basis of correlation analysis, and have been demonstrated using direct survival estimates based on marked fish, they were not detectable using correlation techniques that accurately account for intraseries correlation. There was also weak evidence for an influence of conditions associated with a negative upwelling index at the time chinook salmon enter the ocean. However, because these conditions are associated with high river flows in addition to oceanographic effects, these correlations may merely result from the influence of freshwater flows. To further describe oceanographic influences we computed the principal components of upwelling index, sea level height, and sea surface temperature. The first principle component, which reflected the effects of ENSO conditions in the equatorial Pacific during the previous winter, was significantly correlated with chinook salmon abundance in their final year, and marginally correlated with abundance during the first ocean summer. This work demonstrates new techniques for reducing spurious correlations and the practical difficulties involved in sorting out the multivariate influences on populations subject to remote forcing through oceanographic and meteorological conditions.

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Determination of Factors Affecting Recruitment of Chinook Salmon *Oncorhynchus tshawytscha* in Central California

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Understanding the influences of environment on survival and abundance of chinook salmon *Oncorhynchus tshawytscha* is necessary for management of both fisheries and surface water in central California. The salmon fisheries are managed by allocating predicted preseason abundance between catch and spawning escapement, and flow rates in central California rivers are currently managed to allow adequate flows for spawning and rearing of chinook salmon. Better understanding of environmental influences on salmon populations could improve the ability to forecast preseason abundance and more clearly define the impacts of water management on salmon abundance.

Chinook salmon spawn in freshwater, but spend most of their lives in the ocean. In California's Central Valley, there are four distinct runs of chinook salmon named for the timing of their spawning migrations: fall, late-fall, winter, and spring. Typically over 90% of the spawning salmon are from the fall run, and over 80% spawn in the Sacramento River and its tributaries (USFWS 1987). Fall run chinook salmon migrate upstream July through November, and spawn October through January. Eggs incubate in the gravel October through March, and young fish rear in the streams and migrate downstream December through June (USFWS 1987). Most fish spawn at age 3, with some spawning at ages 2 and 4, and a few fish at age 5 (Dettman et al. 1986, Reisenbichler 1986, Kope 1987). The precocious 2-year-old spawners are primarily males and are called "jacks." While in the ocean, Central Valley chinook salmon are harvested by commercial and recreational troll fisheries. Catches in both fisheries are dominated by 3-year-old fish (Denega 1973, Kope 1987).

In addition to natural production, several hatcheries and spawning facilities produce fish to enhance the fisheries and mitigate for losses of spawning and rearing habitat resulting from water development projects (Fig. 1). The contribution of hatchery production to spawning runs has increased in recent years, and has been estimated to be approximately 15% of the total run in the upper Sacramento River (Reisenbichler 1986), 78% of the run in the Feather River, and 87% of the total in the American River (Dettman and Kelley 1986).

Numerous studies have examined relationships between environmental

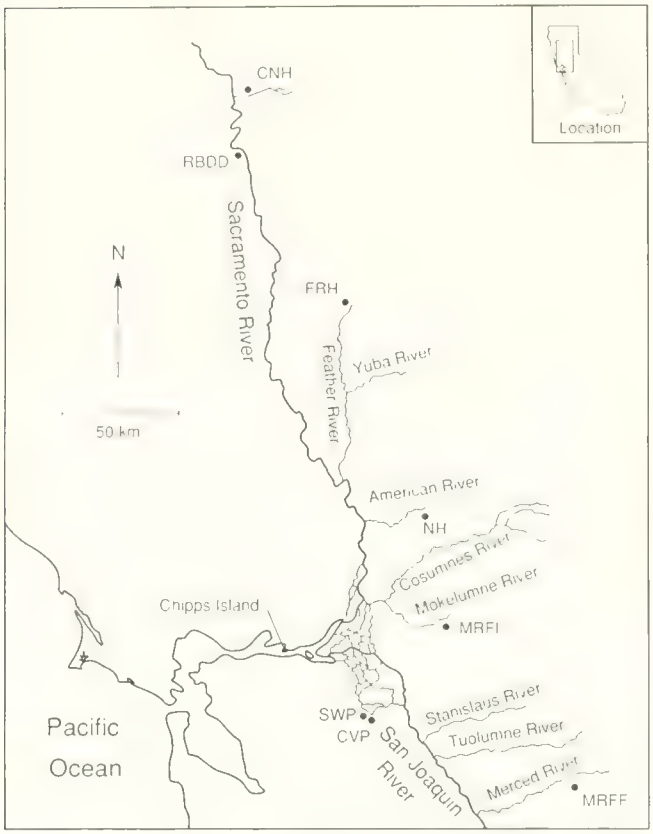

Figure 1

Chinook salmon spawning streams and fish facilities of California's Central Valley. CNH = Coleman National Hatchery; RBDD = Red Bluff Diversion Dam; FRH = Feather River Hatchery; NH = Nimbus Hatchery; MRFI = Mokelumne River Fish Installation; MRFF = Merced River Fish Facility; SWP = State Water Project pumping plant; CVP = Central Valley Project pumping plant.

variables and recruitment or abundance of Pacific salmonids through correlation analysis. Many of these studies have focused on chinook salmon (e.g., Van Hyning 1973, Barton 1980), and a few have dealt with the stock of chinook salmon that spawns in California's Central Valley. Most of these studies have detected environmental influences on recruitment; but in the case of Central Valley chinook salmon, reasonably long time-series of recruitment data have been lacking. Some analysts have therefore used estimates of spawning escapement as a proxy for past recruitment (Dettman et al. 1986, Dettman and Kelley 1986, Reisenbichler 1986, USFWS 1987). In general, these studies have reported positive correlations with flow variables and negative correlations with temperature during the period when the spawners were migrating downstream as smolts. Because of a negative correlation between flow variables and temperatures (Dettman et al. 1986), it is impossible to distinguish between effects of temperature and effects of flow using existing data. Stevens and Miller (1983) used two time-series of smolt estimates based on smolt catches in the delta (Fig. 1), and showed a positive correlation with flows in the previous winter. The most convincing studies used estimates of mortality based on the difference in survival between tagged fish released above the delta and tagged fish released below the delta to show a positive influence of flow rates in the delta and negative influences of temperature and diversions (Kjelson and Brandes 1989, Kjelson et al. 1981, USFWS 1987, Dettman et al. 1986).

In contrast to those of freshwater, potential marine influences on Central Valley chinook stocks have not been explored. Oceanographic conditions off the California coast vary dramatically providing potentially important interannual differences in predators, prey, transport, and ocean temperature during the marine phase of chinook salmon life. The normal pattern of circulation in the northeastern Pacific involves northwesterly winds of varying strength along the coast of California in the spring and summer months which reinforce the geostrophic flow of the California Current and transport surface waters offshore (Mysak 1986, Hickey 1989). This causes varying degrees of upwelling of deeper water and longshore advection of subarctic water along the coast of California and Oregon, which are associated with colder temperatures and depressed sea level heights. The amount of upwelling is estimated by an upwelling index based on winds computed from measured atmospheric pressure gradients (Bakun 1975). Occasional El Niño-Southern Oscillation (ENSO) events, characterized by a warming of equatorial Pacific waters, have a dramatic effect on California coastal waters. These effects may result from either coastal trapped waves which propagate poleward from the Equator, or an atmospheric teleconnection between the Equator and midlatitudes (Emery and Hamilton 1985, Mysak 1986). The former would cause higher sea surface temperatures and sea level heights, but would not necessarily affect Bakun's upwelling index (Enfield and Allen 1980, Emery and Hamilton 1985, Mysak 1986). The latter involves an increase in strength of the Aleutian low-pressure system and a weakening of the north Pacific high-pressure system. Changes in the atmospheric pressure gradients, associated with ENSO events, weaken the northerly winds which results in less upwelling, warmer sea temperatures, higher sea level, and a lower upwelling index (Norton 1987, Mysak 1986). ENSO events and anomalous strengthening of the Aleutian low pressure system may occur at the same time, but each also occurs alone (Emery and Hamilton 1985, Mysak 1986).

Marine and freshwater influences on California Central Valley chinook salmon could be confounded. Large-scale oceanographic and meteorological conditions in

the Pacific have been related to precipitation in California, which could in turn influence flow rates. Markham and McLain (1977) found a positive correlation between California rainfall and sea surface temperature off the coast of Washington. However, rainfall in California is only weakly related statistically to equatorial conditions associated with ENSO events (Douglas and Englehart 1981, Cayan and Peterson 1989, Redmond 1988).

Environmental influences on fish populations are often explored by computing correlations between environmental and population time-series; however, these are computed and the significance of resulting correlations are evaluated in a variety of ways. In attempting to detect environmental influences by computing correlations, the probability of obtaining a significant result is often artificially inflated by two problems: (1) intraseries correlation and (2) multiple tests (cf. Walters and Collie 1988). The latter arises from the fact that many environmental series can be tested for correlation with the population series; hence the probability of falsely identifying a significant relationship is greater than the probability level of each test. Methods exist for dealing with both problems, but we focus on the former here [see Hollowed et al. (1987) and Drinkwater and Myers (1987), for examples of dealing with the latter]. The former, intraseries correlation, is a lack of statistical independence of observations, which implies that the true number of degrees of freedom that should be used in determining the significance of a computed correlation is less than the number of points in the series. There are two steps that can be taken to deal with this problem: (1) removing as much of the intraseries correlation as possible, and (2) accounting for the remaining correlation in the computation of confidence limits.

Removal of intraseries correlation can be accomplished by arbitrarily "pre-whitening" the series (i.e., filtering the series so that correlation between adjacent points is removed) (Box and Jenkins 1976, Fogarty 1988), but is more directly justified when there is a physical basis for doing so and the new series represents a meaningful quantity. In the case of an abundance or catch series, one can compute a recruitment time-series from the original series using deconvolution (Kope and Botsford 1988). Deconvolution is a procedure based on the observation that catch or abundance is a sum over age-classes which is essentially a weighted sum over past recruitment (i.e., a moving average), in which the weighting factors are the (assumed constant) probabilities of survival to each age. If the abundance or catch series is established using a size limit, rather than an age limit, the numbers at each age that are larger than the size limit must also be accounted for in the weighting factors. Deconvolution inverts this summing process to give recruitment in terms of catches or abundances. Deconvolution provides two advantages over using the catch or abundance series without deconvolution: (1) it removes the intraseries correlation due to summing ages in abundance or catch data, and hence provides more conservative estimates of the significance of correlations between recruitment and the environment; and (2) it yields an estimate of recruitment from the abundance or catch data, hence it can also increase the magnitude of estimated correlation coefficients. However, deconvolution cannot yield an exact value of recruitment when noise is present in the abundance or catch data. The error present in the recruitment estimates depends on the error present in the catch or abundance series and on the stability of the deconvolution (Kope and Botsford 1988). Thus, there is a trade-off between the two advantages of removing the effects of multiple age-classes and the disadvantage of amplifying errors that depends on the stability of the deconvolution and the magnitude of measurement errors in abundance. Consequently, deconvolution may not always be useful.

Intraseries correlation is accounted for in the computation of confidence limits by estimating the variance of the computed correlation coefficient in a way that accounts for the intraseries correlation. This often involves using one of the many approximations to an expression originally due to Bartlett (1946) (Box and Jenkins 1976, Chelton 1984, Botsford 1986). This approach is functionally equivalent to adjusting the number of degrees of freedom using a variation of the expression originally due to Bayley and Hammersley (1946) (Sutcliffe et al. 1976, Drinkwater and Myers 1987). We use another method for dealing with this problem that leads to an actual probability of detection that is closer to the specified probability than other methods (Kope and Botsford 1988, Botsford and Wainwright unpubl.).

In spite of the fact that greater intraseries correlation artificially inflates the probability of detecting a significant relationship, some researchers have added intraseries correlation to the time-series before computing correlations. For example, in the freshwater chinook salmon studies cited above, Dettman et al. (1986) and Reisenbichler (1986) used 2-year moving averages of both spawning escapement and environmental variables in an effort to reduce the effects of age structure in the spawning escapement data. Hollowed et al. (1987) used five-point moving averages in their analysis of recruitment patterns in the northeast Pacific. Because the effects of intraseries correlation were not accounted for in either of these studies, the use of moving averages would decrease the probability of detecting real correlations and increase the probability of spurious correlation (Kope and Botsford 1988). Others have used moving averages before computing

correlations, but then have attempted to account for increased intraseries correlation [cf. Drinkwater and Myers (1987), who use a modified form of the Bayley and Hammersley (1946) approach].

The goals of the study reported here are to explore potential environmental influences on chinook salmon populations in California's Central Valley, and to demonstrate the effective use of some recently developed methods of correlation analysis that are more realistic and conservative than those used previously. We identify potential oceanographic environmental influences on these populations and show that the freshwater influences, which were established by direct survival estimates (USFWS 1987, Kjelson and Brandes 1989), are not detectable from correlation analysis of the available environmental and population data.

Data and methods

Environmental data were obtained from four sources. Average monthly streamflow data were obtained from published USGS records for gauging stations at Verona on the upper Sacramento River, Nicholas on the Feather River, and Fair Oaks on the American River. Flow and diversion data for the Sacramento-San Joaquin delta were obtained from the California Department of Water Resources DAYFLOW hydrological model. Data on sea surface temperature at the Farallon Islands, southern oscillation index, and tidal height at San Francisco (37.48 N 122.22 W) were obtained from D. Cayan (Scripps Inst. Oceanography, La Jolla, CA 92037), and calculated coastal upwelling index at lat. 39°N (Bakun 1975) was obtained from A. Bakun (Pacific Fish. Environ. Group, Natl. Mar. Fish. Serv., NOAA, Monterey, CA 93940).

Population data were taken from the recreational fishery, the commercial fishery, and spawner estimates. We used spawner data from the upper Sacramento River, the Feather River, the Yuba River, and the American River. In the available data, adults had been separated from jacks on the basis of length. Fish less than 60.7 cm fork length were taken to be jacks and larger fish were counted as adults. For the period 1970–86, spawning stock estimates were obtained from Pacific Fishery Management Council (PFMC) reports. For the years 1962–69, total fall-run spawners were taken from Fry and Petrovich (1970), and adult spawners were estimated by multiplying the total estimate of fall-run spawners in each stream by the fraction of carcasses classified as adults in the spawning stock surveys. In addition to abundance indices from individual streams, total adult spawners for the entire Central Valley were estimated by multiplying the fraction of adults reported in all spawning stock surveys each year by the number of spawners in all runs for all rivers combined.

Commercial and sport catch south of Point Arena were obtained from PFMC reports for the years 1971–86, and from L.B. Boydstun (Calif. Dep. Fish Game, Region II, Rancho Cordova, CA 95670, unpubl. data) for the years 1962–70. Commercial effort, measured in thousands of landings, and sport effort, measured in thousands of angler days, were obtained or calculated from the same sources. Fishing effort was used to calculate catch-per-unit-effort (CPUE) in an attempt to remove some of the effects of variable fishing effort from the catch data.

Recruitment of year-classes at the beginning of the commercial fishing season in their second year of life was estimated by deconvolution of the abundance indices using the procedure described in Kope and Botsford (1988). This involved calculating the contribution of recruitment in each year to the abundance indices in subsequent years using an age-structured catch and escapement model with population parameters estimated by separable virtual population analysis of marked hatchery fish (Kope 1987). In addition to the recruitment estimates obtained by deconvolution of the individual abundance series, we estimated recruitment by deconvolving the combined abundance series. This combined deconvolution was obtained by adding together commercial catch, sport catch, and total spawning escapement for each year, and deconvolving the combined abundance series (Kope and Botsford 1988).

Examination of the different recruitment estimates revealed that the deconvolved spawner series contained a great deal of high-frequency noise which resulted from the marginal stability of the deconvolutions of spawner indices. Because of differences in the relative contribution of each age-class, the deconvolution of total spawners was inherently much less stable than the deconvolution of adult spawners (Kope and Botsford 1988). Because recruitment estimates from spawners (adults and jacks) and adult spawners were highly correlated with one another (hence probably represent the same signal, and the deconvolved adult spawners contain less introduced error), only deconvolved adult spawners were used as recruitment estimates derived from spawning escapement.

No attempt was made to separate natural production from hatchery fish in the spawning escapement. Because of the large contribution of hatchery fish to the spawning runs (cf., Reisenbichler 1986, Dettman and Kelley 1986) and the straying of hatchery fish (Hallock and Reisenbichler 1979, Sholes and Hallock 1979), accurate estimation of the natural component of the runs was not possible.

Before computing correlations with environmental data, we tested for an influence of density on the pop-

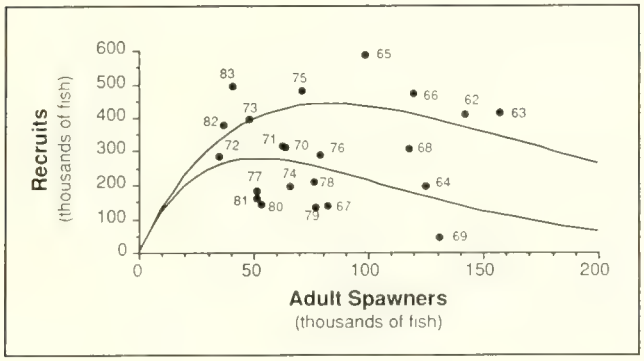

Figure 2

Chinook salmon stock-recruitment curves for the main stem of the Sacramento River. Upper curve was fitted to the data for brood years 1962–66 and the lower curve was fitted to 1967–83.

ulation series. Stock-recruitment relationships for the Sacramento, Feather, and American Rivers were examined by plotting recruitment against spawning stock, and fitting Ricker stock-recruitment curves to the data by the standard linear-regression method. This approach can result in substantial biases in the estimates of stock-recruitment parameters that result from the correlation between recruitment and subsequent spawning stock (Walters 1985, Kope 1988). However, because we use stock-recruitment curves only as a visual aid in interpreting the stock-recruitment data, potential bias was not evaluated.

To examine possible relationships between recruitment and the environment, correlations were computed between time-series of recruitment and quarterly averages of the environmental variables at all lags that had potential biological meaning. These quarterly averages are referred to as: winter, January–March; spring, April–June; summer, July–September; fall, October–December. Correlations with individual stream flows were computed at lags that corresponded to the winter, and to spring while the fish were resident in the streams as fry or migrating downstream. Correlations with delta flows and diversions were computed for the spring while the fish were migrating to sea, and correlations with oceanographic variables were computed from the spring in the year that fish migrated to sea through the summer 2 years later when most fish mature and leave the ocean to spawn. Correlations involving abundance indices (i.e., catch and spawning escapement series) were computed at lags that assumed the indices consisted primarily of 3-year-old fish.

Variability on all time scales can contribute to the variance of time-series and to the magnitude of calculated correlation coefficients. However, variability on greater than annual time scales involves intraseries correlation, which implies the effective number of degrees of freedom is less than the number of years in the series. Linear trends in the time-series reflect variability on time scales that: (a) can easily be removed by detrending, and (b) are not detectable with existing data. We have removed linear trends from our time-series because they may obscure a relationship on faster time scales.

Intraseries correlation due to variability on intermediate time scales was accounted for in evaluating the significance of computed correlation coefficients. The variance of computed crosscorrelation coefficients can be approximated by

$$\mathrm{Var}\,[r_{xy}(t)] \approx \frac{1}{n} \sum_{i=1-n}^{n-1} \left(1 - \frac{|i|}{n}\right) \rho_{xx}(i)\, \rho_{yy}(i) \qquad (1)$$

where n is the number of data pairs, $\rho_{xx}(i)$ and $\rho_{yy}(i)$ are the autocorrelation functions of the two time-series variables at lag i, and $r_{xy}(t)$ is the computed cross-correlation coefficient between the two time-series at lag t (Botsford and Wainwright unpubl., Kope and Botsford 1988). When no intraseries correlation is present, this expression simplifies to

$$\mathrm{Var}\,[r_{xy}(t)] \approx \frac{1}{n} \qquad (2)$$

Because the real values of the autocorrelation functions of time-series variables are unknown, and computed autocorrelation coefficients must be used instead, expression (1) can sometimes produce variance estimates smaller than expression (2). However, expression (2) places a lower bound on the possible variance of computed crosscorrelation coefficients because it approximates the variance in the best possible case, when no intraseries correlation is present. We estimated the significance of computed crosscorrelation coefficients by assuming a normal distribution with variance given by the greater of expressions (1) and (2). This strategy has performed the best in giving appropriate rejection rates in Monte Carlo simulations for independent random series with varying degrees of intraseries correlation (Botsford and Wainwright, unpubl. data).

Results

Exploration of possible density-dependence revealed no clear relationships that could be removed prior to examining the influence of environmental variables. The stock-recruitment relationship for the upper Sacramento River appears to show a decrease in the equilibrium stock size that coincides with the closure of Red Bluff Diversion Dam in 1966 (Fig. 2). This supports the

Table 1

Correlations of chinook salmon population estimates with freshwater flow variables in the Sacramento Valley, California. All correlations significant at the 0.1 level using the uncorrelated series test are shown. Asterisks refer to levels of significance using the test that accounts for intraseries correlation [equation (1)].

Index	Variable	Age of influence	Correlation
Feather River adult spawners	Delta diversions	1st spring	0.456**
Feather River recruits (deconvolved adult spawners)	Delta diversions	1st spring	0.424**
Total adult spawners	Delta inflow	1st spring	0.402*
	Delta outflow	1st spring	0.393*

*$p<0.10$, **$p<0.05$

Table 2

Correlations with combined California Central Valley fall-run chinook salmon spawning stock indices. UPW = upwelling index, SLH = sea level height, SST = sea surface temperature. All correlations significant at the 0.1 level using the uncorrelated series test are shown. Asterisks refer to levels of significance using the test that accounts for intraseries correlation [equation (1)].

Index	Variable	Age of influence	Correlation
Total adults	UPW	1st spring	−0.542***
		1st summer	−0.444*
	SST	3rd spring	−0.427**
		3rd summer	−0.593***
Recruits (deconvolved adults)	SLH	3rd summer	−0.425**
	SST	3rd summer	−0.541***

*$p<0.10$, **$p<0.05$, ***$p<0.01$

argument that the decrease in recruitment is a direct consequence of the dam rather than the result of gradual habitat degradation or increasing fishing pressure (Hallock et al. 1982, Hallock 1983). A similar effect had been observed by Reisenbichler (1986) but he found that the spawning runs resulting from the 1964, 1965, and 1966 brood years were intermediate between the stock-recruit curves associated with the time periods before and after these years. With our deconvolved recruitment estimates, the 1964 brood year appears to have been abnormally low, but 1965 and 1966 appear comparable with earlier years. Data for the Feather River and the American River do not fit stock-recruitment curves as well as the Sacramento River data. Our data include few years before the damming of the Feather River and none for the American River before the construction of Nimbus Dam. On both of these rivers, the hatchery contribution to the spawning escapement is large, hence lack of a clear stock-recruitment relationship is not surprising.

To assess the influence of the freshwater environment on Sacramento Valley stocks, we computed correlations between population variables and environmental variables on three rivers—the Sacramento, the Feather, and the American—as well as the total of these three, and relevant environmental variables. Population variables were total spawners, adult spawners, jacks, and recruitment estimated by deconvolution of adult spawners. We thus tested for environmental effects on all spawners, as well as differential effects on jacks and adults, and recruitment to the adult spawner population. Environmental variables were the flow of each river, total diversions of flow in the Sacramento-San Joaquin Delta, diversions as a percentage of flow, delta inflow, and delta outflow. We present all correlations that were significant at the 0.1 level using the standard uncorrelated series test, and annotate with asterisks the significance of each of these according to the more conservative test that allows for intraseries correlation.

The results (Table 1) provide no evidence for an influence of the freshwater environment on numbers of total spawners, jacks, adults, or adult recruits to these stocks. In fact, the number of correlations significant

Table 3

Correlations between chinook salmon recruitment estimates from ocean abundance indices and environmental variables in Central California. All correlations significant at the 0.1 level using the uncorrelated series test are shown. Asterisks refer to levels of significance using the test that accounts for intraseries correlation [equation (1)].

Index	Variable	Age of influence	Correlation
Commercial catch	UPW	1st fall	0.397*
	SLH	1st fall	−0.415**
	SST	2nd spring	−0.437*
		3rd summer	−0.503**
Recreational catch	SST	1st spring	0.711*
		1st summer	0.484**
		2nd winter	0.578
Commercial CPUE	UPW	1st spring	−0.607
		1st summer	−0.448
Recreational CPUE	SST	1st spring	0.583
		2nd winter	0.500
	UPW	1st spring	−0.453
		2nd winter	−0.357
Recruits (deconvolved commercial catch)	UPW	1st spring	−0.460**
	SST	3rd spring	−0.335
Recruits (deconvolved recreational catch)	SST	1st spring	0.353*
Recruits (combined deconvolution)	UPW	1st spring	−0.476**
	SST	3rd summer	−0.538**

*$p<0.10$, **$p<0.05$

at the 0.1 level is half the number expected if all series were independent (i.e., 4 versus 8 out of 80), and the only correlations significant at the 0.05 level using the conservative test—a positive effect of diversions on Feather River fish—has no apparent physical or biological explanation, because diversions during downstream migration would be expected to have a negative effect on survival. We consider this one a spurious correlation. Lack of correlation with delta diversions and total delta outflow may be due in part to the fact that hatcheries on the Feather and American Rivers have released most of their smolts below the delta since the mid-1970s.

Marine influences on spawners were assessed by computing correlations between the same population variables and upwelling index, sea level height, and sea surface temperature. The resulting correlations (Table 2) are significant at the 0.05 level only for adult spawners and recruitment to the adult spawner population. They show a negative influence of conditions associated with ENSO events (i.e., higher ocean temperatures, higher sea levels) in the third spring and summer, immediately before the adults enter the rivers to spawn. There is also a positive correlation with upwelling index in the first spring and summer, during which smolts migrate downriver, through the delta, and enter the ocean.

We also tested for marine and freshwater influences on catch data from both the commercial and the recreational fishery. We attempted to remove the effects of fluctuations in effort from the catch by computing commercial catch-per-unit-effort and recreational catch-per-unit-effort using the marginal effort data. We computed recruitment estimates from deconvolution of each of these. There is a substantial number of correlations significant at the 0.1 level using the standard test, but none reflect freshwater influences (Table 3). Of the correlations that are significant at the 0.05 level, two are with temperature in the third summer, and the remaining four are in the first marine year, three of them being with upwelling index and the other with sea level height. None of the catch-per-unit-effort variables were significantly correlated with any of the environmental variables using the conservative test.

These results indicate that oceanographic conditions during the first and third years of life may influence

Table 4

Autocorrelations of the Southern Oscillation Index (SOI) and crosscorrelations between SOI and oceanographic variables off Central California. UPW = upwelling index, SLH = sea level height, SST = sea surface temperature, PC = principal component. Underlined correlations correspond to an influence of previous SOI on winter oceanographic conditions off California.

	SOI	UPW	SLH	SST	1st PC
Winter SOI					
−9 mo	0.552***	0.478***	−0.205	0.000	−0.253
−6 mo	0.730***	0.261	−0.211	−0.093	−0.279
−3 mo	0.811***	0.208	−0.439**	−0.405**	−0.390*
0	1.000***	0.667***	−0.651***	−0.573***	−0.712***
3 mo	0.256	0.380*	−0.342*	−0.305	−0.449**
6 mo	0.031	−0.140	−0.270	−0.108	−0.168
9 mo	−0.110	0.231	−0.239	−0.133	10.163
12 mo	−0.131	−0.034	−0.042	−0.103	−0.078
Spring SOI					
−9 mo	0.112	0.340*	−0.102	−0.088	−0.202
−6 mo	0.115	0.113	−0.117	−0.330	−0.321
−3 mo	0.256	−0.050	−0.169	−0.165	−0.030
0	1.000***	0.393*	−0.268	−0.298	−0.414*
3 mo	0.825***	0.022	−0.297	−0.328	−0.326
6 mo	0.688***	0.246	−0.540***	−0.402**	−0.406*
9 mo	0.562***	0.424**	−0.389	−0.518***	−0.531***
12 mo	−0.224	−0.094	−0.067	−0.212	−0.129
Summer SOI					
−9 mo	−0.154	0.143	0.190	0.029	−0.070
−6 mo	0.031	−0.091	−0.037	0.007	0.092
−3 mo	0.825***	0.390*	−0.242	−0.191	−0.353
0	1.000***	0.269	−0.337*	−0.350*	−0.448**
3 mo	0.785***	0.200	−0.573***	−0.572***	−0.507***
6 mo	0.761***	0.428**	−0.433**	−0.535***	−0.544***
9 mo	0.109	0.197	−0.147	−0.337	−0.301
12 mo	−0.214	−0.256	−0.021	0.047	0.090
Fall SOI					
−9 mo	−0.110	−0.175	0.063	0.128	0.197
−6 mo	0.688***	0.426**	−0.324	−0.246	−0.406*
−3 mo	0.785***	0.305	−0.211	−0.192	−0.309
0	1.000***	0.164	−0.441**	−0.344*	−0.346
3 mo	0.835***	0.504***	−0.630***	−0.479***	−0.604***
6 mo	0.114	0.233	−0.341*	−0.314	−0.385*
9 mo	−0.152	−0.269	−0.123	0.043	0.010
12 mo	−0.072	0.263	−0.044	0.087	−0.031

*$p<0.10$; **$p<0.05$; ***$p<0.01$

these stocks of chinook salmon. However, because the correlations are with three oceanographic variables rather than consistently with one, they are somewhat difficult to interpret in terms of a causal mechanism. To attempt to solve this problem, we sought a single indicator of variability in the coastal ocean. We computed the principal components (Harris 1975) of variability in sea surface temperature, sea level height, and upwelling index, in the hope that they would have a meaningful physical interpretation. The resulting first principal component is larger than the second and third by about a factor of two, depending on season, and its loading is approximately equal for all three variables (positive for sea level height and ocean temperature and negative for upwelling index). Positive values of sea level height and surface temperature are consistent with the higher latitude effects of ENSO events as would be propagated by coastal trapped waves, but the negative value of upwelling index would require atmospheric teleconnection (recall the upwelling index is not a measure of actual upwelling, but an estimate based on atmospheric pressure

Table 5

Correlations between first principle component of the oceanographic variables and estimated total age-3 abundance (recreational catch + commercial catch + adult spawners) of chinook salmon in Central California.

	Season	First year	Second year	Third year
Total abundance	Winter	0.289	0.101	−0.151
	Spring	0.356*	−0.317	−0.354
	Summer	0.274	−0.139	−0.482**
	Fall	−0.115	0.114	0.080
Deconvolved total abundance	Winter	0.121	0.239	−0.139
	Spring	0.361*	−0.202	−0.319
	Summer	0.166	0.017	−0.480**
	Fall	−0.177	0.108	0.097

*$p<0.10$; **$p<0.05$

differences, cf. Emery and Hamilton 1985, Mysak 1986).

To test whether the first principle component was actually related to ENSO events, we computed lagged correlations between it and the Southern Oscillation Index (SOI), a primary indicator of ENSO events (Table 4). The results show that the first principal component is highly correlated with the Southern Oscillation Index during the previous winter. Also, in all but one instance (sea level height and spring SOI) the three oceanographic variables are correlated with SOI in the previous winter in the way that would be expected from their loading in the first principle component.

To further simplify interpretation, we attempted to use a single indicator of abundance. In correlations computed thus far, no single population variable had a demonstrably stronger relationship to environmental variables tested. We therefore used the sum of commercial catch, recreational catch, and spawner estimates as a single indicator of annual population abundance. For the corresponding deconvolved estimate we use the deconvolution of this combination of these three series, the deconvolution that was previously shown to provide the best estimate of recruitment (Kope and Botsford 1988).

The results using the first principle component and the total abundance estimate (Table 5) indicate an influence of ENSO-related conditions during the summer of the third year ($\alpha \leq 0.05$) and provide weak evidence for an influence of ENSO-related conditions during the first spring ($\alpha \leq 0.10$). These relationships are reflected in both the total abundance and the estimate of recruitment to total abundance obtained through deconvolution. The estimate of total abundance is also correlated with previously identified oceanographic variables. The correlations with spring upwelling are -0.478 ($\alpha \leq 0.10$) and -0.511 ($\alpha \leq 0.01$) for total abundance and deconvolved total abundance, respectively. The correlations with summer ocean temperature are -0.551 ($\alpha \leq 0.10$) and -0.540 ($\alpha \leq 0.05$) for total abundance and deconvolved total abundance respectively.

Discussion

The negative correlation between abundance in the third year and the first principle component of the oceanographic variables is consistent with observed effects of ENSO events on coastal oceanographic conditions and fish populations. Productivity in the California Current, as represented by zooplankton biomass, has long been known to be inversely correlated with sea surface temperature (Reid et al. 1958, Reid 1962). High productivity has traditionally been attributed to upwelling, but this explanation was recently questioned by Chelton et al. (1982) who proposed that higher zooplankton biomass resulted from increased equatorward flow in the California Current. The two proposed mechanisms are difficult to separate because conditions conducive to upwelling would also increase the strength of the California Current. However, whether colder water comes from the subarctic or from deeper coastal waters, it is higher in nutrients than the warmer surface waters, hence colder ocean temperatures in the winter and spring are associated with higher productivity in the California current (Chelton et al. 1982). Effects on productivity would be most noticeable during strong ENSO events. For example, total catch and average weight of chinook salmon landed in the commercial and sport fisheries were lower during the recent 1983 ENSO event (PFMC 1984, Pearcy et al. 1985, Johnson 1988).

The weak correlation between marine environmental variables during the first summer and indices of

abundance and recruitment is of the opposite sign to that expected on the basis of these relationships between the environment and productivity. However, it is possible that because juvenile fish feed on different prey than adult fish, shifts in prey distributions in warm-water years may result in higher growth and survival rates for juveniles. Northward shifts in the distribution of larval clupeids have been documented in warm-water years (Radovich 1959, 1961), and larval anchovies were found closer to shore than usual during the 1983 ENSO (Brodeur et al. 1985). Larval clupeids are a principal prey of juvenile chinook salmon (Peterson et al. 1982, Pearcy et al. 1985). Data taken off the Oregon coast show no significant difference in feeding by first-year chinook salmon between 1983, a warm-water year, and the other years 1980–85 (Brodeur and Pearcy In press).

The results obtained here for freshwater influences during the downstream migration in the first year have greater implications for the general methodology of correlation analysis in fisheries than for the dependence of salmon survival on environment. Other direct observations—the fact that differences in survival between marked fish released above the delta and marked fish released below the delta is correlated with flow over 10 years (USFWS 1987)—provide convincing evidence for a negative effect of low flows in the delta. Our results merely underscore the potential for falsely identifying a suspected relationship using standard methods for computing correlations. A dependence of abundance on freshwater variables was not detected when intraseries correlation was removed, rather than artificially added, and when it was taken into account in computing correlation coefficients. Fortunately, for this case there have been direct measurements of survival, and we need not rely solely on correlation analysis of abundance and environmental data.

Although a freshwater effect is not detectable in correlations with these freshwater variables, it may provide a partial explanation for the weak correlation seen between population variables and oceanographic conditions during the first year. During the spring, the first principle component of oceanographic variables is highly correlated with total delta inflow—flow in the Sacramento, Feather, and American Rivers (0.687, 0.577, 0.610, and 0.631, all significant at the 0.01 level using the conservative test). Thus the correlation between the first principle component of oceanographic variables during the first spring may be due to occurrences in freshwater, rather than oceanographic influences.

The various relationships implied in the results of this study provide a view of remote forcing of the North American marine and terrestrial environment that may be of general utility in examining the effects of environmental variability on other species. Events in the equatorial Pacific appear to drive the oceanographic and meteorological environment in the eastern North Pacific and western North America. Autocorrelations in the SOI (Table 4) indicate that the Equatorial events are spring to winter events (i.e., in column 1, seasons within any spring-to-winter period are correlated with each other, but none are correlated with seasons in any other spring-to-winter period). The rest of Table 4 indicates that these events influence conditions in our coastal ocean only in the following winter. This "winter only" aspect of this correlation is consistent with results relating an index of atmospheric pressure conditions on the west coast of North America, the Pacific North American index to events in the equatorial Pacific (Horel and Wallace 1981). Mysak (1986) attributed this "winter only" aspect of the equatorial/midlatitude teleconnection to the requirement for strong westerlies between the equator and midlatitudes in order to advect the atmospheric Rossby waves responsible for the teleconnection to the northeast. These westerlies exist only during the winter. The covariability among our three oceanographic variables (i.e., the fact that UPW is as important as SLH and SST in the loading on the first principle component) suggests an atmospheric teleconnection with equatorial ENSO rather than a wave propagating poleward from the Equator (cf. Emery and Hamilton 1985, Mysak 1986). These variables are also related to winter rainfall in central California. For example, annual rainfall in Sacramento is significantly correlated with the first principle component and the upwelling index in winter. Flows through the Sacramento-San Joaquin Delta the following spring are in turn correlated with that rainfall, as well as winter oceanographic conditions. This remote forcing on a global scale and the associated covariability of marine and terrestrial variables further confound the identification of causal mechanisms from these kinds of data.

However, even direct measures of survival versus environmental variables do not necessarily identify mechanisms unequivocally. Covariation between flow rates, diversions, and reversed flows in the lower San Joaquin River continue to obscure the true cause of lower run size in the San Joaquin River system (Kjelson and Brandes 1989, USFWS 1987).

The differences in results between standard methods and the new methods used here are a rough measure of how much more conservative they are. At the 0.10 level, for example, the more conservative method of computing the variance of the estimate of correlation coefficient yielded significant correlations roughly half as often as standard methods (Tables 1–3). These results, together with simulations that show that the combination of equations (1) and (2) yield the prescribed

false detection rates (α) (Botsford and Wainwright unpubl.), imply that this correction for intraseries correlation or a similar one should be used in correlation analysis.

Deconvolution also reduced the number of significant correlations. For example, at the 0.10 level, using the standard test, there were only 6 significant correlations with deconvolved variables, whereas there were 21 significant correlations for corresponding variables that were not deconvolved. The fact that this ratio is lower when the more conservative correlated series test is used (5 with deconvolution and 13 without) is to be expected because the test itself accounts for some of the intraseries correlation. Although the number of significant correlations is less with deconvolution, we cannot recommend its use in all situations. Deconvolution can have two positive effects on correlation analysis: (1) It can provide a better estimate of recruitment, and (2) it can reduce intraseries correlation, hence the variance of the estimate of correlation coefficient (Kope and Botsford 1988). However it can also have a negative effect. If the deconvolution is marginally stable, the abundance data is noisy, or the coefficients of the deconvolution are inaccurate, deconvolution can lead to a poorer estimate of recruitment. In the results presented here, deconvolution introduced some additional significant correlations and reduced the magnitude of existing correlations (although they remained significant at the same level). This suggests that the deconvolved series may be a poorer proxy for recruitment than the raw abundance series, and that this detracts from the removal of intraseries correlation.

The practical implication for chinook salmon managers of the correlations obtained here is primarily a recommendation of where to focus further research rather than a means of immediately achieving a dramatic improvement in management. Because these stocks are managed by annually attempting to control effort based on an attempt to predict abundance, an understanding of the factors affecting abundance is necessary. The relationship between salmon populations and oceanographic conditions during the third year has an R^2 of 0.23, and hence would not produce predictions that could substantially improve catch. It also does not hold for oceanographic conditions in the previous 3-month period, hence there is little potential for long-term prediction. However, the results do indicate two potentially useful relationships between environment and abundance. Our understanding of these relationships could possibly be improved to the point that they could be useful in management. The ability to estimate numbers at each age in catch and escapement would improve our ability to determine potential oceanographic effects as well as provide a possible predictor of catch (i.e., 2-year olds). The current practice of differentiating jacks from older fish on the basis of size leads to considerable uncertainty that could be removed by determining age through hard parts or separation of modes in the size distributions each year. Also, the existence of a demonstrated freshwater effect implies we should attempt to remove that effect from the data before searching for an oceanographic effect. However, this is complicated by the fact that an unknown fraction of the annual catch is produced by hatchery fish that were trucked below the delta for release, and hence not exposed to that effect. Better knowledge of where and when fish are released could provide the basis for removal of the effects of variable release numbers and release strategies from the data before searching for oceanographic effects.

In general, results from correlation analyses in fisheries will always contain an element of doubt and, by themselves, are probably not strong enough evidence of causal relationships that management should be based on them. Poor performance of past relationships argue for less dependence on them (Sissenwine 1984, Drinkwater and Myers 1987, Walters and Collie 1988), however, as we have shown here, there are ways of improving the reliability of correlation analyses. For example, smoothing with moving averages should be done only when the level of measurement noise warrants it, and it should always be accompanied by some means of accounting for the intraseries correlation introduced. Although we agree that the resulting statistical relationships do not, by themselves, provide a solid basis for management, we are not as pessimistic as some others (e.g., Walters and Collie 1988) regarding the utility of correlation analysis. It supplies information on patterns that allows formulation of hypotheses that can then be tested through direct means. It increases the probability of detection of relationships that might otherwise be missed. Fisheries analysts cannot afford to dismiss the opportunities it provides, but should use it only as exploratory analysis (cf. Bakun 1990, Botsford et al. 1989).

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Abstract.–Between 1980 and 1987 in Massachusetts Bay, 156 individual fin whales *Balaenoptera physalus* were photographically identified using variations in natural markings and scars. Of these, 98 (62.8%) were observed more than once, and 70 (44.9%) were photographed in 2 to 8 different years. On average, 49.2% of whales seen in a year were resighted at least once during that year, and 44.5% were observed the following year. Within a year, the observed occupancies (the period between first and last sighting) of resighted individuals varied from 1 to 197 days (mean 46.1), while the number of separate days on which individuals were sighted ranged from 1 to 12 days (mean 2.5). However, given the strong bias in photographic effort towards other species in the region, it is likely that rates of within-season occurrence and annual return are considerably underrepresented in the data. Overall, the results suggest some similarity between the population characteristics of fin whales and those of the sympatric humpback whale *Megaptera novaeangliae*, although data from whaling catches and from radio telemetry point to the existence of major differences between the two species.

Population Characteristics of Individually Identified Fin Whales *Balaenoptera physalus* in Massachusetts Bay

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In recent years, techniques for the identification of individual cetaceans using variations in natural markings and scars have permitted investigations of the biology and behavior of many species (recently summarized in Hammond et al. 1990). Some of these studies have yielded detailed descriptions of the structure and patterns of migratory movement of some populations. Until recently, similar studies of fin whales *Balaenoptera physalus* had been hampered by the lack of a technique with which to reliably identify individual whales, and by the tendency of observers to concentrate on more accessible species whose ranges overlap that of the fin whale.

As a result, the high-latitude distribution of the fin whale remains poorly understood despite extensive hunting this century. On the one hand, whaling data and information from some radio telemetry studies have shown that fin whales sometimes undertake extensive movements. For example, a whale radio-tagged by Watkins et al. (1984) travelled 1700 km across the Irminger Sea in 9.5 days. Discovery tag returns suggest that Antarctic fin whales, at least over the course of several seasons, may have high-latitude ranges that encompass as much as 90 degrees of longitude (Brown 1962). In contrast to this, a whale tagged by Watkins et al. (1981) in Prince William Sound, Alaska, exhibited short-term site fidelity, remaining in a restricted area for at least 28 days. At a broader level, whaling data led Sergeant (1977) to characterize the composition of the North Atlantic fin whale population as a "patchy continuum." Mitchell (1974) believed that some spatial separation of stocks existed, but that different populations moved latitudinally with the seasons, with some whales moving south in winter to occupy the summering areas of others. Data from CeTAP (1982) generally support this idea of a seasonal shift in the population.

Mayo (1982) and Mayo et al. (1985) presented a technique for the identification of individual fin whales using variations in natural features as well as prominent scars. This technique has since been adopted by a number of observers in the western North Atlantic (Clapham 1987, Agler et al. 1990), and has been used by us to study the population characteristics of fin whales observed in Massachusetts Bay during the period 1980–87. We present here the results of this study, including evidence that fin whales on a high-latitude feeding ground exhibit patterns of seasonal occurrence and annual return that are in some respects similar to those shown for humpback whales *Megaptera novaeangliae*.

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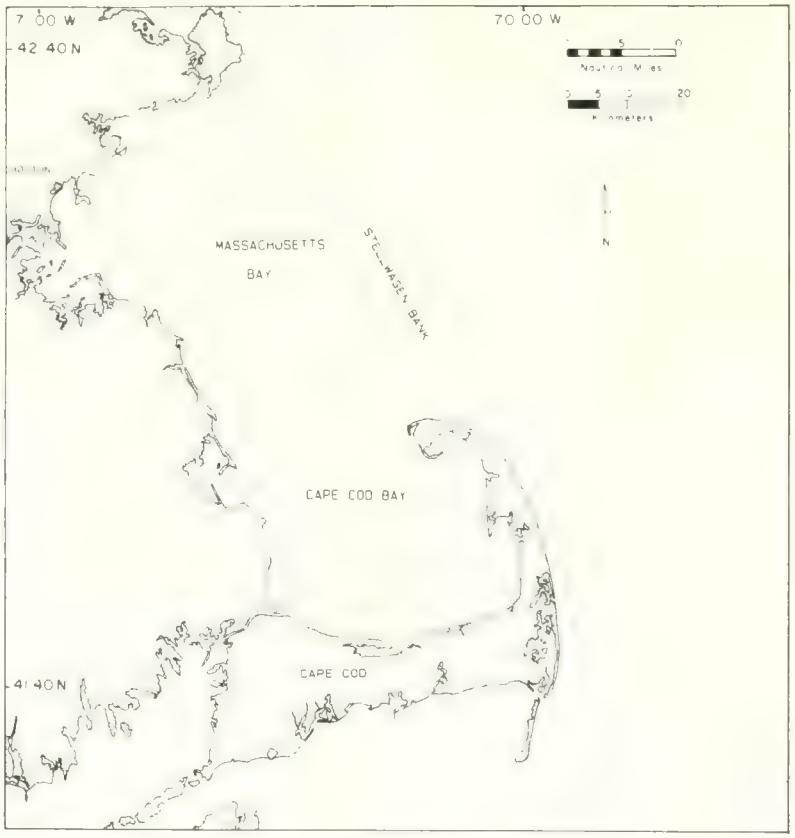

Figure 1
Fin whale study area.

Methods

The observations in this study were conducted in the coastal region dominated by Massachusetts Bay and Cape Cod Bay (Fig. 1) between the years 1980 and 1987 inclusive. Observations were made from 30-m commercial whalewatching vessels operating between April and October of each year from Provincetown, Massachusetts. Beginning in the autumn of 1983, additional cruises were made from a 12-m diesel-powered research vessel and, beginning in the autumn of 1985, from a 14-m auxiliary ketch. The total number of cruises conducted during the study period was 5979, 97% of which were made by whalewatching vessels.

Search patterns were in most cases non-random and non-systematic. This was particularly true of the whalewatching vessels, where search tracks were decided by the captains based upon where most whales had been seen the previous day or trip. Search effort directed specifically at fin whales varied considerably. Because humpback and (during the spring) right whales *Eubalaena glacialis* were preferred by the whalewatching vessels, opportunities to obtain usable photographs of fin whales occurred only incidentally except during periods when the preferred species were less abundant or absent. An exception were four fin whales that exhibited large, permanent scars that were easily noticeable from a distance of 100 m or more. Because these whales were among the few that could be readily recognized by all observers in the field, they were much more likely to be photographed, and confirmation of identity could be achieved with poorer quality photographs than those taken of unscarred whales.

Individual fin whales were identified using variations in natural markings, as described in Clapham (1987), Hawvermale (1987), and Agler et al. (1990). Major features used included the shape of the dorsal fin, the light-colored wash of pigment on the right side of the head (the "blaze"), and the V-shaped pattern of light pigment behind the blowholes and extending down both sides of the whale (the "chevron"). Scars were also used. A full definition of features and a description of the technique can be found in Agler et al. (1990).

Fin whales exhibit asymmetry in their coloration, with greater variability in features on the right side of the head than the left; consequently, while some whales were identified using both right and left sides, an individual was not considered matchable if only the

left side was photographed. Because fin whales generally have less marked variations in their features than do humpback or right whales, and because a series of photographs of high quality are generally required to successfully identify an individual, we adopted a conservative approach in our matching: only photos of excellent quality were used, and a match was considered confirmed only if three features were common in photographs of both sightings.

Photographs were taken with a 35-mm camera equipped with a 200-mm, 300-mm or 400-mm lens, power winder, and recording databack. Kodak Tri-X or T-Max film (both rated at ISO 400) was used. Copies of photographs were sent to the North Atlantic Fin Whale Catalogue at College of the Atlantic in Bar Harbor, Maine, for analysis of the movement of individual whales outside our study area.

Definitions

The following terms are used in this report:

Occupancy The sum of the resighting intervals of an individual whale within years, i.e., the number of days between the first and last sighting of a whale in a particular year. We do not assume that an individual was necessarily present in the study area for all or part of the period between sightings.

Occurrence The temporal distribution of an individual whale in the study area, expressed as the total number of separate days on which the whale was observed.

Resighting interval The interval, in days, between successive sightings of an individual whale within a particular year.

Results

During the period 1980–87, a total of 156 fin whales were individually identified. While many other animals were photographed, this number represents only those whales that were sufficiently well-marked and well-photographed to ensure that the file contained no duplicates. A total of 98 individuals (62.8%) were observed more than once, 70 (44.9%) of which were photographed in more than one year. The photographs shown in Figure 2 provide one example of the features used to identify an individual whale in two different years.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

While fin whales were sometimes observed between the beginning of November and the end of February, none were photographed during this period in any year. (In 1979, only two fin whales were photographed, both of which were subsequently resighted).

Table 1 shows the number of individuals observed for each year of the study period, the percentage of these animals that were photographed on more than one day in that year, and that were reidentified in each subsequent year. The occurrence of identified fin whales during 1987 (the year with the largest number of cruises) is shown in Figure 3. This temporal distribution is broadly representative of other years with a similar level of effort. Table 2 summarizes resighting intervals, grouped by 10-day periods, for 1985, 1986 and 1987 combined (the 3 years with the greatest vessel effort).

Occupancy was calculated for each whale that had been observed more than once in a year (individuals seen only once or not at all in the year were excluded). Observed occupancies (n = 159, including two or more occupancy periods for individuals who were resighted in more than one year) ranged from 1 to 197 days (mean 46.1 days, SD 47.407). The mean number of days in a year that individual fin whales were photographed (occurrence) was calculated (including individuals observed on only one day, but excluding individuals not observed in the year). Observed values (n = 264) ranged from 1 to 12 days (mean 2.5 days, SD 2.011).

Of the 70 individual fin whales photographed in more than one year, 26 were observed in 2 years, 15 in 3 years, 14 in 4 years, 7 in 5 years, 3 in 6 years, 3 in 7 years, and 2 in 8 years. (These figures include the two individuals identified in 1979.) Table 3 summarizes the sighting histories of these whales.

Discussion

A major problem confounding interpretation of the data presented here is the relatively low level of effort involved in this study. An appreciation of the difference in effort directed at fin whales and at humpback whales (the whalewatching vessels' preferred species) can be gained by comparing the respective ratios of sightings to individual identifications, i.e., the total number of whales recorded (whether photographed or not) versus the number of sightings for which not only was a photograph taken, but where the photograph was good enough to positively identify the individual. For humpback whales, this ratio is consistently about 1.2:1 for all years. For fin whales, however, the ratio ranged from 11:1 in 1986 (a year with unusually low numbers of humpback whales) to 83:1 in 1981. The mean for all years was 32:1. These ratios reflect two factors. Firstly, far fewer fin whales were approached than hump-

Figure 2

An example of a year-to-year match of an individual fin whale in Massachusetts Bay. The photos show catalogue number 0143 in 1983 (top two photos) and in 1987 (bottom two photos).

Table 1

The number of individual fin whales (n) identified in Massachusetts Bay for each year of the study period, and the percentage of those individuals that were reidentified within the same year, and in each subsequent year. For example, of the 22 individuals identified in 1981, 50.0% were seen more than once that year, 59.1% were reidentified in 1982, and 50% in 1983. The mean of all same-year resightings is 49.2%. The mean of all consecutive year values (e.g., 1980–81, 1981–82) is 44.5%.

	1980	1981	1982	1983	1984	1985	1986	1987
1980 $n = 21$	33.3%	38.9%	38.9%	50.0%	44.4%	33.3%	66.7%	61.1%
1981 $n = 22$		50.0%	59.1%	50.0%	40.9%	45.5%	40.9%	45.5%
1982 $n = 38$			42.1%	42.1%	39.5%	42.1%	47.4%	47.4%
1983 $n = 33$				48.5%	42.4%	36.4%	54.5%	60.6%
1984 $n = 38$					50.0%	36.8%	44.7%	50.0%
1985 $n = 31$						58.1%	54.8%	51.6%
1986 $n = 67$							52.2%	37.3%
1987 $n = 64$								59.0%

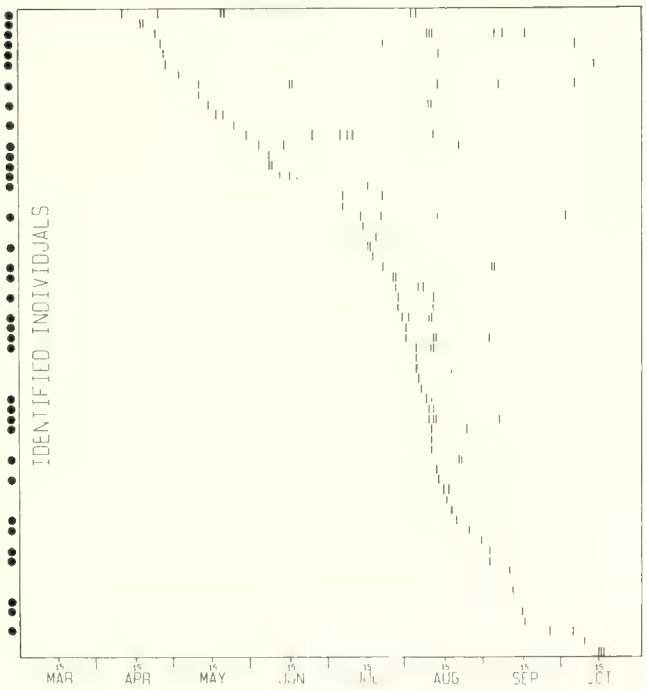

Figure 3

Observed temporal occurrence of individual fin whales in Massachusetts Bay during 1987. Individual whales are ordered (top to bottom) by date of first sighting; each row of marks represents the dates on which one individual was seen during the year. A black dot to the left of the vertical axis signifies that the individual concerned had been observed in at least one previous year of the study period.

Table 2

Resighting intervals, grouped by 10-day periods, of individual fin whales photographed in Massachusetts Bay for the three years 1985, 1986 and 1987 combined. The zero-interval category encompasses whales that were observed only once during a year.

Interval (days)	No. of intervals
0	81
1–10	146
11–20	24
21–30	14
31–40	9
41–50	6
51–60	4
61–70	2
71–80	2
81–90	2
91–100	2
101–110	0
111–120	0
121–130	0
131–140	0
141–150	0
151–160	1
161–170	1
171–180	1

Table 3

Sighting histories of individual fin whales observed in Massachusetts Bay in more than one year of the study. O = observed. Note: 0180 and 0394 were also observed in 1979.

No.	1980	1981	1982	1983	1984	1985	1986	1987	No.	1980	1981	1982	1983	1984	1985	1986	1987
0017	O	O	O	O		O	O	O	0227			O	O			O	
0027	O	O	O	O	O	O		O	0228			O	O			O	
0045	O					O	O		0230			O		O			
0061	O	O		O			O	O	0232			O				O	
0062		O	O			O	O		0233			O		O	O		O
0064	O				O		O	O	0241			O	O				O
0068	O		O						0261	O		O				O	O
0069	O			O				O	0266			O		O	O		
0081	O	O	O	O	O	O	O	O	0267			O	O		O	O	O
0086	O			O	O			O	0275			O			O	O	O
0089	O	O		O	O	O	O	O	0281			O		O		O	O
0090		O	O						0286			O					O
0093	O		O		O		O		0287				O	O			
0096	O							O	0299				O		O		
0110	O	O							0303				O		O	O	
0113				O			O		0318				O	O			
0114	O					O	O		0319				O	O		O	O
0126		O	O		O	O			0322				O	O		O	O
0131		O					O		0334				O			O	O
0137	O				O		O		0357					O		O	
0141		O	O						0367					O	O	O	O
0143		O	O	O			O	O	0391					O		O	O
0146		O	O	O	O	O		O	0394					O	O	O	O
0174		O	O		O	O			0420					O		O	
0179	O	O		O			O		0434					O		O	
0180		O	O	O	O	O	O	O	0443					O		O	O
0183		O	O	O	O			O	0452					O	O		
0189		O	O	O	O	O		O	0512						O	O	
0213			O	O		O	O	O	0520						O	O	O
0215			O	O	O	O		O	0521						O		O
0218			O		O				0542						O	O	
0222	O		O	O	O		O	O	0575							O	O
0224			O				O		0582							O	O
0225			O			O	O		0584							O	O
0226			O	O			O		0592							O	O

backs. Furthermore, while a humpback can often be recognized from a single poor-quality photograph, identification of most individual fin whales requires a series of high-quality photographs which must be taken from approximately the same position relative to the whale.

Despite this, the frequency with which individual fin whales were resighted is high. Roughly half of the fin whales seen in one year were seen again the same season, and about half were also resighted the following year. Resighting intervals provide some evidence for a degree of residency on the part of some whales, and of bimodal occupancy by others. However, the many gaps in the sighting histories of individuals are difficult to interpret. Do the gaps represent whales that were resident in the area for extended periods but were not photographed, or do they indicate movement to other areas between sightings? At this point, we can say only that, given the obvious bias in effort, it seems likely that rates of within-season occurrence and annual return of fin whales in Massachusetts Bay are considerably under-represented in our data. When only 1 out of every 83 fin whales sighted is identified (as occurred in 1981), it is unlikely that even an individual which remained in the area for many weeks would be recaptured more than a few times. This is supported by the fact that the subset of individuals towards which there was clear observer bias—those bearing large, prominent scars—were among the most frequently observed animals during this study. For example, whale number 0081, named "Braid" (an animal with very large propeller scars on its left side), was observed in all 8 years, with a mean occupancy of 116 days, and mean occurrence of 6 days.

It is clear, however, that many of the gaps in our sighting histories of individual whales represent real absences from the area. Resightings of individuals outside our study area confirm that the summer ranges of these whales are often, if not regularly, extensive. In a preliminary analysis of photographs from the North Atlantic Fin Whale Catalogue, Agler et al. (1990) report a number of instances of movement of individuals between Massachusetts Bay and the waters of Maine and the Bay of Fundy. It is possible that some individuals undertake extensive movements outside the Gulf of Maine, but the current lack of observer effort beyond this region precludes investigation of this idea.

From the regional perspective of this study, it is tempting to compare the results reported here with the much more complete information available on Gulf of Maine humpback whales and to conclude that the two populations are broadly similar in their patterns of occurrence and distribution. The annual return rate of humpback whales to Massachusetts Bay is extremely high, with as many as 85% of individuals observed in one year returning the next (Mayo 1983, Mayo et al. 1988). While no individual humpback remains in Massachusetts Bay for an entire season, many appear to spend prolonged periods in the area between making wider forays elsewhere in the Gulf of Maine (Clapham and Mayo 1987, Mayo et al. 1988). Other humpbacks are observed less often, and presumably frequent other habitats for much of the year, a fact which reflects considerable variation among individuals. It is also clear that overall individual fidelity to the Gulf of Maine is maternally directed (Clapham and Mayo 1987).

It is not unreasonable to expect that fin whales might exhibit similar patterns of occurrence. Given that the distribution of fin and humpback whales in high latitudes must be predominantly related to the distribution of their prey (Payne et al. 1986), it is to be expected that the occurrence of both species should be characterized by individuals returning repeatedly, both during a season and from year to year, to consistently productive habitats such as Massachusetts Bay. From the standpoint of energetics, it would make little sense for an individual to abandon an area of high productivity and search elsewhere if the resources found in the former habitat were adequate for its needs, although it is possible that, as suggested by Watkins et al. (1984), social imperatives play an important role in the movement of individuals.

Overall, the data presented here suggest that there are more similarities than differences in the high-latitude population characteristics of humpback and fin whales, although data from other sources suggest that significant differences between the two species do exist. In addition to the above-mentioned studies which documented extensive movements on the parts of individuals (Brown 1962, Mitchell 1974, Watkins et al. 1984), other observers have noted evidence for spatial segregation by length in certain areas (Mackintosh 1942, Mitchell 1974, Rorvik et al. 1976, Sergeant 1977), a phenomenon that has not been demonstrated for humpbacks. Our own data are regional in nature and do not permit us to address these broader questions of population structure at the oceanic level. However, with increased photographic effort in other areas, studies based upon the identification of individual fin whales should provide clearer insights into the population biology of this species in the North Atlantic.

Acknowledgments

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Abstract.– A symbiotic nemertean worm found on spiny lobsters is described and compared with other members of the genus *Carcinonemertes*. The new species of *Carcinonemertes* has a relatively large basis, stylet, anterior and posterior proboscis chambers, and a voluminous seminal vesicle. In addition, lateral intestinal diverticula project anterior to the level of the middle proboscis chamber. These characters distinguish this species from others in the genus.

The life-history patterns of six species of *Carcinonemertes* appear related to the developmental timing of host embryogenesis. Portunid crabs with a short duration of embryogenesis are infested by the species *C. carcinophila* and *C. mitsukurii*. The worms settle only on mature female hosts; after eclosion the worms migrate to the branchial lamellae of the host where they lie dormant until the host oviposits a new clutch. Cancrid and grapsid crabs with an intermediate duration of embryogenesis are infested by the species *C. epialti* and *C. errans*. The worms settle on both sexes of crabs and are sexually transmitted to female hosts. At eclosion, the worms die or regress and migrate to the limb axillae. Lithodid crabs and panulirid lobsters with a long duration of embryogenesis are infested by *C. regicides* and *C. wickhami*. The nemerteans settle on ovigerous hosts and die or leave the host after eclosion.

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Carcinonemertes wickhami n. sp. (Nemertea), a Symbiotic Egg Predator from the Spiny Lobster *Panulirus interruptus* in Southern California, with Remarks on Symbiont-Host Adaptations

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Nemerteans of the genus *Carcinonemertes* (Kölliker, 1845) are specialized symbionts of decapod crustaceans. Several species of *Carcinonemertes* eat the eggs of their hosts (Humes 1942, Kuris 1978, Wickham 1980, Roe 1984); and this trophic habit may be diagnostic for the genus (Wickham 1986, Wickham and Kuris 1988). Three species have been described from the west coast of North America: *C. epialti* Coe, 1902; *C. errans* Wickham, 1978; and *C. regicides* Shields, Wickham, et Kuris, 1989. Nemerteans from the spiny lobster were distinct from these species in both morphology and life history. The nemertean from the spiny lobster represents the undescribed species listed by Wickham and Kuris (1985) for that host.

Here we describe the egg predator *Carcinonemertes wickhami* n. sp., from the broods of the spiny lobster *Panulirus interruptus* (Randall), from southern California. The distinctive morphological characters of the new species are discussed, and aspects of the life history of the new species are presented with those of other members of the genus.

Materials and methods

Spiny lobsters *Panulirus interruptus* were collected by University of California divers using SCUBA. Lobsters were caught by hand. Pleopods of infested female lobsters were examined macroscopically; those containing worms were excised and immediately placed in seawater. Nine ovigerous lobsters were examined in 1982, and 10 in 1988. Three of the lobsters collected in 1988 were held for 4–7 days after eclosion (postovigerous); they were then dissected and examined for worms. Particular attention was paid to the limb axillae, branchiae, and branchial chambers. Nemerteans found in the broods of lobsters were gently manipulated onto slides for measuring and photomicrography. Worms were measured with an ocular micrometer in a dissecting microscope. They were then covered with a coverslip, and various measurements of internal features were taken with an ocular micrometer in a compound microscope. Hatched nemertean larvae were examined alive. Measurements are in

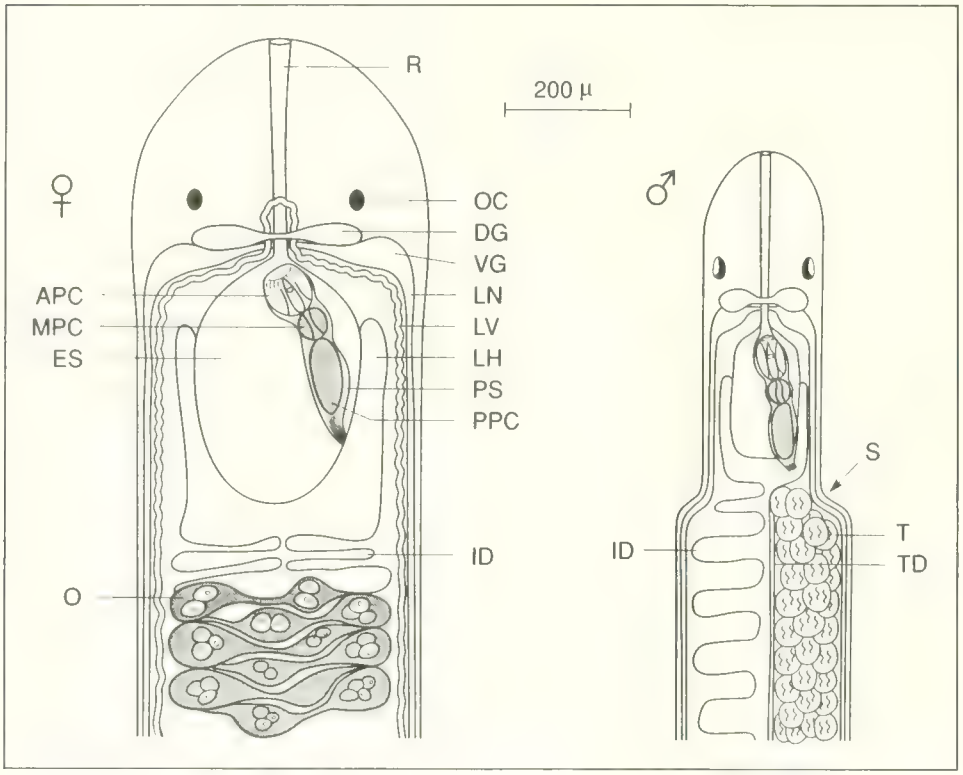

Figure 1
Composite drawing of female (left) and male (right) *Carcinonemertes wickhami* from *Panulirus interruptus*. Note the reproductive system of the male is represented on the right side of the body, while the digestive system is figured on the left side, and the circulatory system has been omitted for clarity. Key to labels: APC = anterior proboscis chamber; ES = foregut; DG = dorsal ganglia; ID = intestinal diverticula; LH = lateral horn of intestine; LN = lateral nerve cord; LV = lateral blood vessel; MPC = middle proboscis chamber; OC = ocellus; O = ovary; PPC = posterior proboscis chamber; PS = proboscis sheath; R = rhynchodaeum; S = shoulder; T = testis; TD = Takakura's duct system (vasa eferens, vas deferens, seminal vesicle, gonoduct); VG = ventral ganglion. Bar = 200 µm.

micrometers unless otherwise stated. Means are given with ranges in parentheses.

Worms were fixed in hot AFA (acetic acid, formaldehyde, alcohol) or 5% formalin-seawater. Representative specimens were sectioned at 10 µm and stained with hematoxylin and eosin.

Description

Carcinonemertes wickhami new species (Figs. 1–13)

Female (3 living specimens; 7 specimens, sectioned) Body slender, ciliated; orange color. Shape filiform with rounded anterior end, blunt posterior end; found in tough, glistening parchment-like sheaths, but often free. Sheaths with minute refractile lapilli, grainy in texture, slightly longer than accompanying worm. Worm length 10–30 mm, up to 50 mm when fully extended, average width 400 (345–456). Two ocelli anterior to prominent dorsal and ventral cerebral ganglia. Ocelli cup-shaped, conspicuous, 36 (34–39) long by 28 wide; located 145 (126–168) from anterior end. Distance between ocelli 257 (172–368). Rhynchodaeum and esophagus passing between commissures of the dorsal and ventral ganglia. Anterior portions of lateral blood vessels fuse between dorsal and ventral cephalic commissures in a single anterior loop. Posterior portion of lateral blood vessel ventral to lateral nerve cord near anus. Proboscis with three chambers, dorsomedial or lateral to posterior part of foregut. Anterior proboscis chamber 98 (84–112) long by 80 (70–87) in diameter, with basis and stylet. Basis large, 40 (36–42) long by 14 in posterior diameter. Single large stylet, 20 (19–20) long, with posterior knob-like proximal piece. Middle proboscis chamber granular in appearance, 47 (39–59) in diameter. Posterior proboscis chamber long, slender, 125 (112–140) long by 42 (28–56) in diameter; glandular, with lumen. Foregut joins rhynchodaeum at or just posterior to cephalic commissure. Posterior part of foregut robust, 380 (280–517) long, by 244 (182–345) in diameter; muscular, ciliated. Musculature of foregut attached laterally to longitudinal musculature of body wall. Posterior part of foregut leading directly into intestine; pyloric stomach absent. Intestine with a pair of lateral diverticula extending anterior to level of middle proboscis chamber. Intestine posterior to foregut with numerous paired, unbranched diverticula. Anus terminal. Ovaries elongate, with medial and lateral lobes; numerous, regularly distributed between intestinal diverticula. Ovaries with indistinct ovarian pores. Ovarian field begins immediately posterior to posterior part of foregut, extends to near anus. In section, ovaries with appearance of four rows in immature and mature females (compare Figure 4 with Figure 1); but ovaries really in two distinct rows (Fig. 1). Ovaries

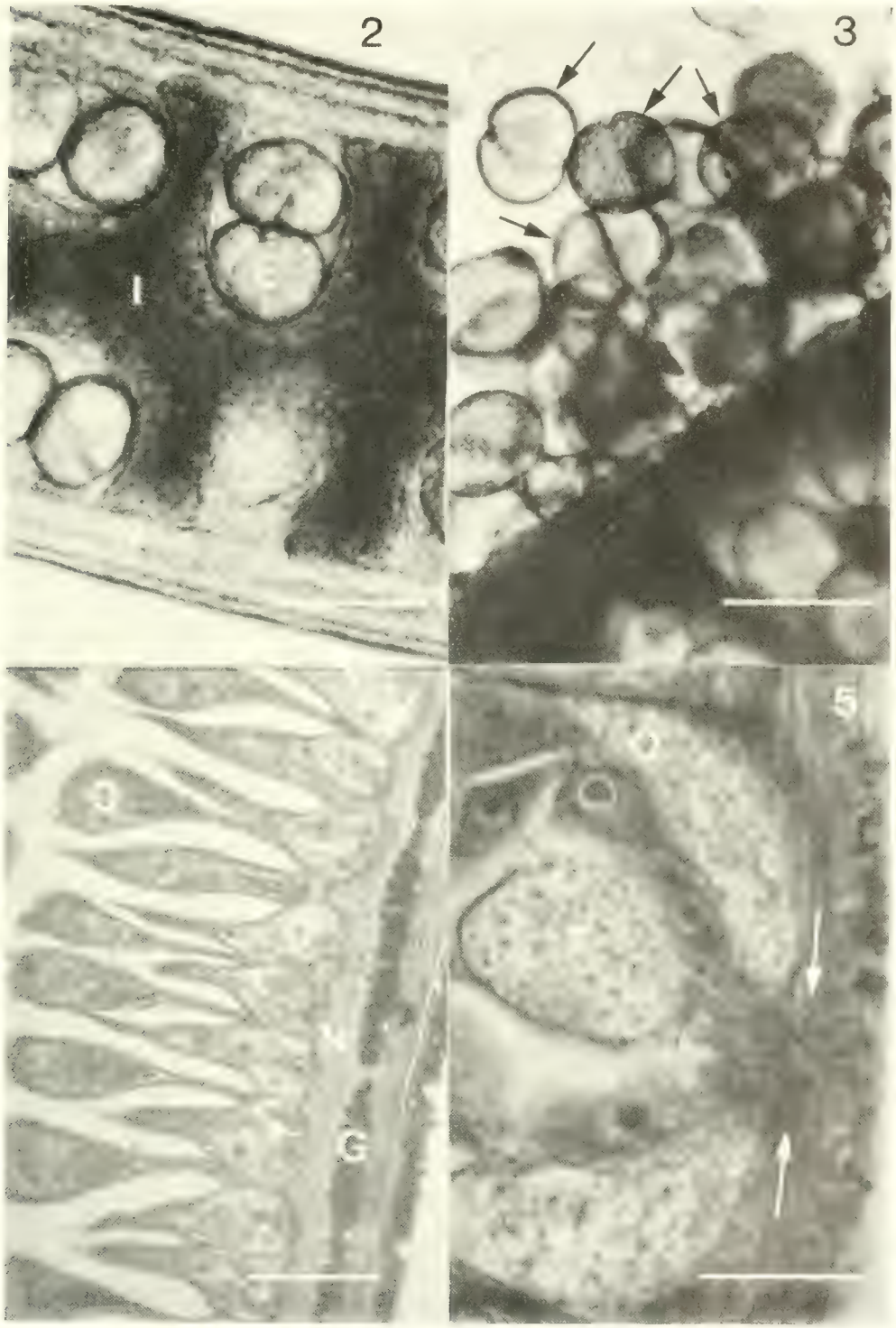

Figure 2
Fertilized embryos (E) within the ovary of a female *Carcinonemertes wickhami*; intestine (I) and lateral nerve (N). Bar = 100 μm.

Figure 3
Artificially released embryos of *Carcinonemertes wickhami*; fertilized embryos (arrows). Bar = 100 μm.

Figure 4
Sagittal section through the ovarian region of a female *Carcinonemertes wickhami*. The ovaries (O) appear in four rows but they are actually in two (only one side of worm in figure; compare with Figure 1); lateral nerve (N); submuscular glands (G). Bar = 100 μm.

Figure 5
Indistinct ovarian pore (arrows) on the lateral, submarginal surface of a female *Carcinonemertes wickhami*; egg (E); ovary (O); Bar = 50 μm

variable in size in relation to developing ova, 196–294 long by 92–168 in diameter. Eggs faint pink, deposited in a flimsy, mucous matrix (cf. sac) secreted by female.

Male (3 living specimens, incomplete observations on 2 additional specimens) Similar in gross morphology to female; differences include: diameter of worm expands at the beginning of the testicular field, setting off the anterior portion of the worm as a relatively slender head (cf. shoulder). Color pinkish white. Ensheathed with female or free in egg mass. Length 5–18 mm, up to 20 mm when fully extended. Ocelli located

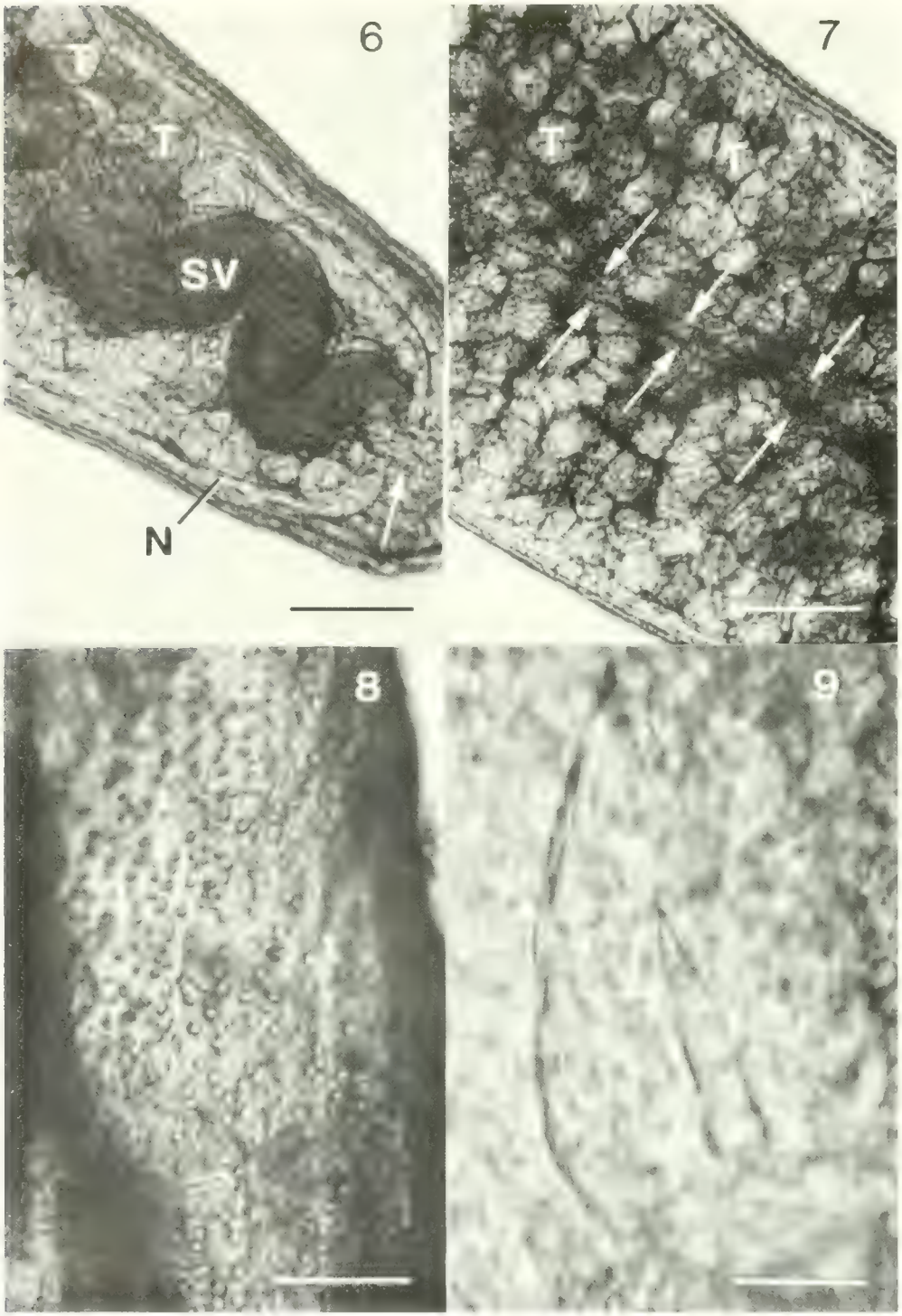

Figure 6
Posterior portion of Takakura's duct system from a live, mature male *Carcinonemertes wickhami* showing the enormous seminal vesicle (SV) and gonoduct (arrow); testis (T); lateral nerve cord (N). Note the lack of testes in the region surrounding the seminal vesicle. Bar = 100 μ.

Figure 7
Anterior portion of Takakura's duct system from a live mature male *Carcinonemertes wickhami*. The vas deferens (arrows) is distinctly visible; testis (T). Bar = 100 μm.

Figure 8
Granular, lapillated sheath of a female *Carcinonemertes wickhami*. Bar = 50 μm.

Figure 9
Stylet (arrow) and basis of *Carcinonemertes wickhami* lying in the anterior proboscis chamber. Bar = 25 μ.

163 (126–196) from anterior end; distance between ocelli 162 (151–182). Anterior proboscis chamber 79 (70–84) long by 57 (56–59) in diameter. Posterior proboscis chamber 149 (112–196) long by 47 (42–56) in diameter. Posterior part of foregut 196 (168–252) long by 151 (112–196) in diameter. Testicular field begins immediately posterior to posterior portion of foregut, extends posteriorly to terminate 659 (632–690) from cloaca. Testes located between intestinal diverticula; not found adjacent to proximal portion of the seminal vesicle. Mature testes with striated appearance, ovoid, 60 (56–70) long by 52 (42–62) in diameter. Takakura's

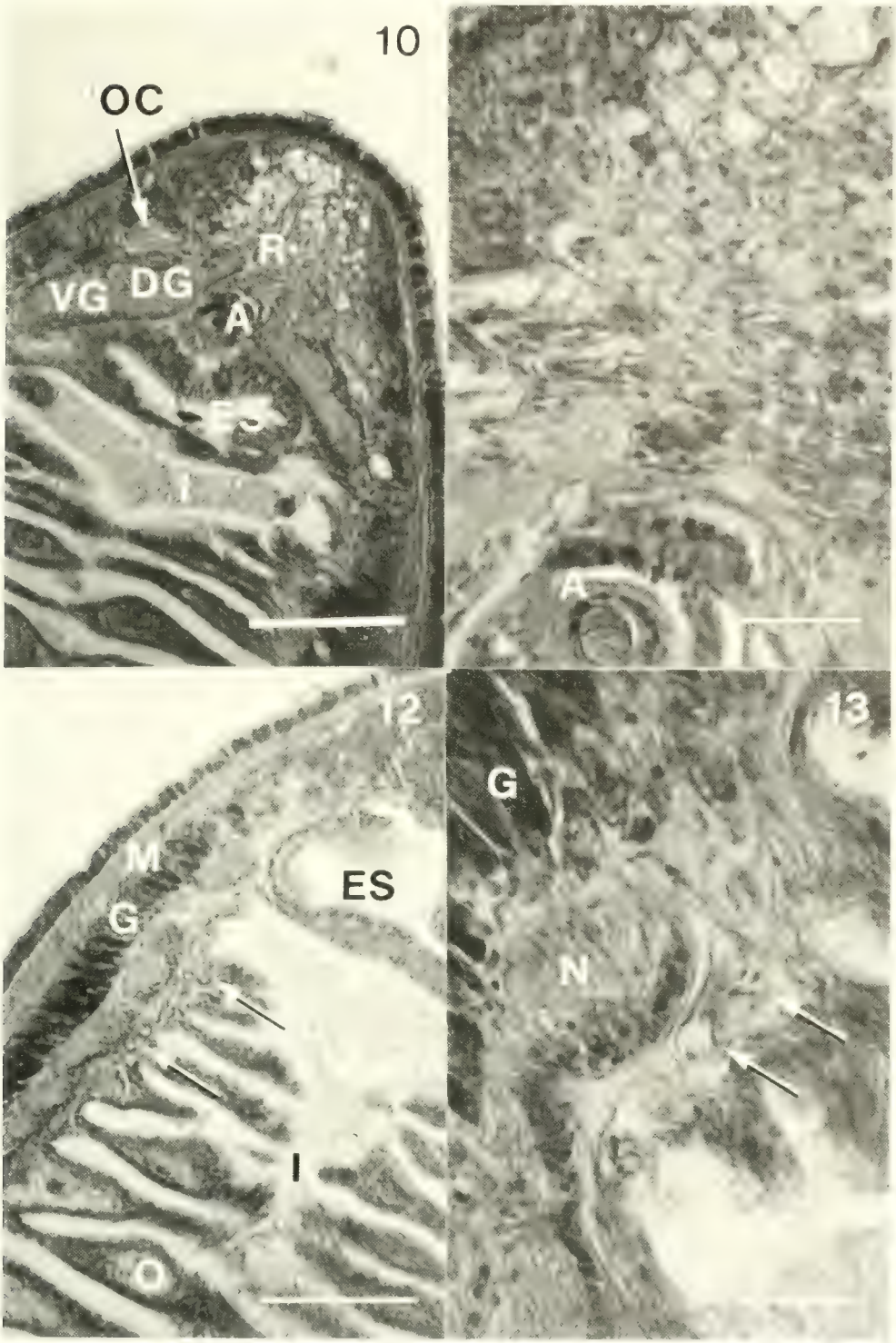

Figure 10
Sagittal section of the anterior end of a female *Carcinonemertes wickhami*; anterior proboscis chamber (A); ventral portion of the dorsal ganglion (DG); foregut (ES); intestine (I); ocellus (OC); rhynchodaeum (R); and ventral ganglion (VG). Bar = 100 μm.

Figure 11
Detail of the cephalic region of *Carcinonemertes wickhami* in sagittal section. Note the criss-crossing of the cephalic musculature; anterior proboscis chamber (A). Bar = 25 μm.

Figure 12
Sagittal section through the anterolateral portion of a female *Carcinonemertes wickhami*. Lateral blood vessels (arrows; see also Figure 13); foregut (ES); prominent submuscular glands (G); intestine (I) with intestinal diverticula; muscle layer (M) with longitudinal and circular muscles; and ovary (O). Bar = 100 μm.

Figure 13
Detail of the lateral blood vessels (from Figure 12) in the weakly developed parenchyma anastomosing between the intestinal diverticula (right) and the lateral nerve (N); submuscular gland (G). Bar = 25 μm.

duct system distinct, extending from anteromost testes to gonopore. Seminal vesicle single, voluminous, near posterior end, 421 (402–460) long by 96 (58–115) in diameter, "S" or "double-S" shape in appearance, surrounded by thick muscular region (= ejaculatory muscles?). Anus and gonoduct empty into common, ciliated cloaca with muscular sphincter.

Larvae (based on 5 living specimens) Typical hoplonemertean. Body completely ciliated, color white with

pink anterior. Larva spherical or ovoid, length approximately 84 (74–92). Anterior and posterior cirri or tufts, approximately 56 long. Two ocelli.

Taxonomic summary

Parasite *Carcinonemertes wickhami* (NEMERTEA: Carcinonemertidae).

Host California spiny lobster *Panulirus interruptus* (Randall). Found on 6 of 9 lobsters in July 1982, and 2 of 10 lobsters in August 1988.

Site of infestation Egg-bearing pleopods of female lobsters. Sometimes attached to bases of uropods or pleopods adjacent to the egg mass. Not found in/on branchiae, branchial chamber, arthrodial membranes, or limb apodemes of nonovigerous females. Not found on male lobsters.

Type locality CALIFORNIA: Santa Barbara, near More Mesa, depth of 5 meters.

Holotype USNM Helm. Coll. #80501: 1 slide—small female holotype in serial section (frontal); and larger female paratype in serial section. Date host collected: 7 July 1982.

Paratype USNM Helm. Coll. #80502: 1 vial—4 male worms; 1 vial—5 female worms; 1 vial—several egg strings attached to setae and eggs of host. Paratypes from two hosts. Hosts collected: More Mesa, 8 August 1988. Additional material in authors' collections.

Etymology The species is named in honor of Dr. Daniel E. Wickham for his contributions to the biology of the genus.

Definition Hoplonemertea, Monostilifera, Carcinonemertidae. Long, filiform nemerteans, up to 50 mm long by 400 μm wide. Anterior proboscis chamber large, 98 (84–112) long by 80 (70–87) in diameter in females; 79 (70–84) long by 57 (56–59) in diameter in males. Basis robust, 40 (36–42) long by 14 basal diameter. Stylet large, with posterior hub, 20 (19–20) long. Posterior proboscis chamber long, slender, 125 (112–140) long by 42 (28–56) in diameter in females; 149 (112–196) long by 47 (42–56) in diameter in males. Posterior portion of foregut large, robust, up to 517 long by 345 in diameter. Lateral intestinal diverticula extending to level of middle proboscis chamber. Worms often found in tough, lapillated, parchment-like sheath. Female with indistinct ovarian pores. Diameter of male expands as a "shoulder" at the beginning of the testicular field. Males with voluminous seminal vesicle, up to 460 long by 115 in diameter. Hoplonemertean larva, 84 (78–92) long.

Diagnosis *Carcinonemertes wickhami* most closely resembles *C. mitsukurii* Takakura, 1910, *C. carcinophila carcinophila* (Kölliker, 1845), and *C. c. imminuta* Humes, 1942 (Table 1). These four nemerteans have relatively large adult forms. *Carcinonemertes wickhami* can be distinguished from these large species by its relatively larger basis and stylet, anterior and posterior proboscis chambers, larger foregut, and the voluminous seminal vesicle in males (Table 1). *Carcinonemertes wickhami* can be distinguished from the smaller species (*C. australiensis* Campbell, Gibson et Evan, 1989; *C. coei* Humes 1942; *C. epialti* Coe, 1902; *C. errans* Wickham, 1978; and *C. regicides* Shields, Wickham, et Kuris, 1989) by its larger size, relatively larger anterior and posterior proboscis chambers, the voluminous seminal vesicle in males, and by the presence of 2 rows of ovaries rather than 4 rows as in *C. coei* (Table 1).

Remarks and discussion

Humes (1942) and Wickham and Kuris (1988) have reviewed the genus *Carcinonemertes*, and Shields et al. (1989) and Campbell et al. (1989) have recently amended the family. Seven species are presently recognized, one of which contains two subspecies, *C. carcinophila carcinophila* and *C. c. imminuta* (Table 1). *Carcinonemertes wickhami* is the eighth species to be described, the second species described from a palinuran, and the first species described from southern California. It represents the undescribed species from the spiny lobster listed by Wickham and Kuris (1985).

Adult *C. wickhami* are often aligned along the tangled egg-bearing setae of the pleopods. The location of the worm along with its photonegative behavior make it difficult to observe this relatively large species in the egg mass of the lobster. Other species of *Carcinonemertes* also exhibit photonegative behavior (*C. epialti* and *C. regicides*; Shields et al. 1989).

The larger species of *Carcinonemertes* are well-muscled in comparison with the smaller species which exhibit a predominantly muco-ciliary movement (Shields et al. 1989). Active thrashing and peristaltic movements were noted in *C. wickhami*. Males were observed to form figure-8 loops by active muscular contraction. *Carcinonemertes wickhami* is also strongly adhesive, a property shared by *C. errans* and *C. regicides* but not by *C. epialti* and *C. mitsukurii* (Shields, pers. observ.).

Carcinonemertes wickhami, *C. australiensis*, and *C. regicides* have large anterior proboscis chambers,

Table 1

Morphological characteristics of the eight species of *Carcinonemertes*. APC = anterior proboscis chamber; PPC = posterior proboscis chamber. Measurements are in microns (except length which is mm) and represent means. NS = not seen.

Species	Sex	Length	Basis	Stylet	APC	PPC
C. australiensis Campbell, Gibson, et Evan, 1989	F&M	7.0	40.0	15–18	75	90 × 45
C. c. carcinophila (Kölliker, 1845)	F	70.0	25.0	9.0	NS	63 × 48
	M	20.0				
C. c. imminuta Humes, 1942	F	16.5	21.0	7.3	40–50	139 × 47
	M	8.7				
C. coei Humes, 1942	F	6.6	22.7	8.7	>32	78 × 47
	M	4.2				
C. epialti Coe, 1902	F&M	4.0–6.0	30.0	13.5	61–68	
C. epialti * (Shields, pers. observ.)	F	4.3	31.2	14.5	75	63 × 41
	M	2.2				
C. errans Wickham, 1978	F&M	4.0–6.0	35.2	11.0	>46	100 × 50
C. mitsukurii Takakura, 1910	F	30.0	27.0	8.0	48**	86 × 28**
	M	10.0				
C. regicides Shields et al., 1989	F	2.1	40.0	17.0	76	82 × 62
	M	1.6				
C. wickhami n. sp.	F	30.0	40.0	20.0	98	125 × 42
	M	10.0			79	149 × 47

*ex. *Cancer antennarius*
**Shields, pers. observ.

bases, and stylet apparatus. These species prey on large host eggs. In addition, the morphology of the stylet of *C. wickhami* is similar to that of *C. regicides* (i.e., in the form of a broad, flat dagger). The above adaptations may allow penetration of the thick outer coat of these large eggs (Wickham and Kuris 1988).

The presence of ovarian pores may be of taxonomic value to the genus. Distinct ovarian pores were not observed on female *C. wickhami*. Similarly, Stricker (1986) did not find distinct ovarian pores on *C. epialti*. Takakura (1910) and Shields et al. (1989) reported distinct ovarian pores from *C. mitsukurii* and *C. regicides*, respectively. The ovarian pores of *C. regicides* are typically found prior to ovulation, but are not apparent prior to oviposition (Shields et al. 1989); *C. mitsukurii* appears to follow a similar pattern (Shields, pers. observ.).

The larvae of *C. wickhami* resemble the typical hoplonemertean larval form (Gibson 1972, p. 150), and are similar to the larvae of *C. epialti* in gross morphology (Stricker and Reed 1981). Larvae most likely undergo direct development into the juvenile stage upon settling onto their host (Stricker and Reed 1981). The larva of *C. wickhami* is similar to that of *C. carcinophila*, *C. epialti*, and *C. regicides*; the larvae do, however, differ in size. *Carcinonemertes wickhami* has the smallest larva yet described for the genus.

Mature *C. wickhami* were found only in the broods of ovigerous lobsters. Further, these nemerteans have been collected only from lobsters with eggs in relatively advanced stages of development (development of eye placodes initiated—8 of 19 lobsters examined). No nemerteans were recovered from 6 lobsters with relatively early broods nor from 3 lobsters held for dissection after eclosion. *Carcinonemertes wickhami* does not appear to migrate to the branchial chamber and into the branchiae after host eclosion, nor does it move to the limb apodemes and axillae (see below).

Three distinct life-history patterns have emerged for six of the eight species of *Carcinonemertes*. These patterns appear related to the developmental timing of host embryogenesis (oviposition to eclosion): embryogenesis in various reptantian decapods can be of short (e.g., 13–16 days), moderate (e.g., 40–120 days), or long duration (e.g., 120–300+ days). In addition, life-history patterns may be useful taxonomic characters as few differences in morphology aid in distinguishing between species.

1 Portunid crabs have a short duration of embryogenesis (Churchill 1919, Sandoz and Rogers 1944). Carcinonemertid larvae settle primarily on ovigerous female crabs where they quickly metamorphose and mature. After eclosion, adult worms migrate to the

branchial chamber, encyst between the branchial lamellae, and lie dormant until the female crab oviposits (Humes 1942). Adult worms then migrate back to the clutch (Humes 1942, Hopkins 1947). Two species of *Carcinonemertes* follow this pattern: *C. carcinophila* and *C. mitsukurii*.

2 Embryogenesis of cancrid and grapsid hosts is of moderate duration (Kuris 1971, Roe 1979, Wickham 1980, Shields et al. In press). Carcinonemertid larvae settle on male and female crabs, metamorphose into juveniles, and migrate to the limb apodemes, axillae, and abdomens of their hosts. Juveniles transfer from male to female crabs during host copulation (Wickham et al. 1985). The juveniles then lie dormant, absorbing amino acids and other nutrients (Roe et al. 1982), until the host oviposits her clutch. Juvenile worms then migrate into the egg clutch and mature after eating crab eggs. Two nemerteans follow this pattern: *C. errans* and *C. epialti*.

3 Spiny lobsters and king crabs brood their eggs for long periods (Marukawa 1933; Shields, pers. observ.). Nemertean larvae settle, metamorphose, and mature only on ovigerous female crabs. Adult worms die or leave the host at eclosion. Circumstantial evidence suggests that planktonic larvae may, in at least one species (*C. regicides*), reinfect hosts immediately upon hatching (Kuris et al. In prep.). Two species follow this pattern: *C. regicides* and *C. wickhami*.

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Abstract.—Age and reproductive parameters were determined for bottlenose dolphins *Tursiops truncatus* captured in shark nets off Natal, on the southeast coast of southern Africa. Calibration of dentinal and cemental growth-layer-group (GLG) readings, using a known-age captive-born dolphin, indicated that dentinal and cemental GLGs are deposited annually, at least up to an age of 6 years. Female growth in length and mass and male growth in length are best described by von Bertalanffy growth curves. Male growth in mass is characterized by a growth spurt at puberty. Most growth occurs during the suckling years. Both sexes reach physical maturity and their asymptotic size—243 cm and 176 kg for males, and 238 cm and 160 kg for females—between 12 and 15 years. Both males and females may reach ages in excess of 40 years, based on counts of GLGs in teeth. Females attain sexual maturity between 9 and 11 years of age, 2 or 3 years earlier than males. Mating and birth are seasonally diffuse, although there is a peak of births in summer. The calf is born at a mean length and mass of 103 cm and 13.8 kg, respectively, after a gestation period of about 1 year. Lactation lasts between 18 months and two years, although there is evidence of an extended mother and calf association of up to 3 years. Postpubertal female ovulation rate is 0.28/year, and the estimated calving interval is approximately 3 years. There is no evidence that females become reproductively senescent with increasing age. Estimates of population replacement suggest that man-induced mortality may equal or exceed the replacement rate.

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Age, Growth, and Reproduction of Bottlenose Dolphins *Tursiops truncatus* from the East Coast of Southern Africa

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Many populations of small inshore delphinids are exploited either directly or indirectly (Mitchell 1975, Beddington et al. 1985, Northridge and Pilleri 1986), and their continued survival depends on adequate management based on knowledge of their life history. In this context, knowledge of the reproductive parameters of a species is important in formulating management and conservation proposals. In particular, the reproductive biology of females is crucial to an understanding of the likelihood of a species' survival.

An estimated 900 bottlenose dolphins *Tursiops truncatus* inhabit Natal, along a stretch of some 400 km of coastal waters, southeast of southern Africa (Ross et al. 1989). Between January 1980 and December 1987, a minimum of 212 of these animals were captured in noncommercial inshore nets set to catch and deplete the numbers of large sharks off bathing beaches (Cockcroft and Ross In press). The catch of dolphins in anti-shark nets is of concern in the continued survival of these animals off Natal (Ross et al. 1989, Cockcroft and Ross In press).

Feeding studies on the bottlenose dolphins off Natal have shown that groups are segregated by sex and size. Lactating females and their calves frequent and feed in the nearshore zone, adolescents feed slightly further offshore, while resting females and adult males feed still further offshore (Cockcroft and Ross 1990). Consequently, the catch of these animals in the shark nets is biased, with calves less than 2 years old and lactating females constituting almost 60% of the total (Cockcroft and Ross In press). Other age and sex classes, particularly pregnant females and adolescents, are, therefore, probably underrepresented.

This study was undertaken to establish the reproductive potential of bottlenose dolphins off Natal, as part of a more extensive investigation of the natural history of these animals and severity of the threat to the population through capture in shark nets. Where appropriate, recognition is given to the effects of biases in sex and size composition, noted above, which reduce the accuracy of deductions made from catch data (Perrin and Reilly 1984).

Materials and methods

Routine necropsies were performed on all bottlenose dolphins retrieved from the Natal shark nets. Biological and morphological parameters, including sex, total length, and mass were recorded for each animal, based on the recommendations of Norris (1961) and Mitchell (1975). Collected organs were preserved in 10% formalin and later transferred to 50% ethyl alcohol for storage.

Testes were excised, weighed after removal of the epididymis, and the dimensions (length × maximum height × width) measured. The epididymis was visually checked for the presence of sperm and scored as present or not; no microscopic evaluation was undertaken. Testes from young animals (combined testis mass $\lesssim$100 g) were preserved whole, while only a section removed from the bigger testis of older males was kept. Standard histological slides, approximately 5 μm thick and stained with haemotoxylin and eosin, were prepared from whole testes or from three locations (outer, middle, and inner) of sections of large testes. From each slide the diameter of a minimum of 10 circular seminiferous tubules was measured at a magnification of 125 using an ocular reticule, to assess testis development stage.

Lactating females and calves caught together were considered mother and calf pairs. Both left and right ovaries were routinely collected and preserved from all females. These were sectioned serially at about 1-mm intervals, and the number and dimensions of corpora albicantia in each ovary and the presence and dimensions of any corpus luteum were recorded. The length and mass of any fetus present in the uterus was recorded before preservation. Mammary glands were assessed for the presence of milk and, for most lactating females, the width, length, and depth measured.

The state of physical maturity of animals was assessed from the degree of fusion of the epiphyses to the centra of midthoracic vertebrae (immature = unfused, maturing = fusing, and mature = fused). The brain mass of neonates and calves was measured directly. That of adults was estimated by filling the skull with coarse dry sand, after first sealing all apertures with adhesive tape, measuring the volume of sand in a measuring cylinder, and assuming this to represent the brain mass.

Age was determined from the number of growth-layer groups (GLGs; *sensu* Perrin and Myrick 1980) counted in the dentine and cement of longitudinal thin sections of teeth. The largest mandibular or maxillary teeth were used. Numerous methods of obtaining thin sections were employed, including hand grinding on 1200-grade abrasive paper or between glass sheets using jewelers rouge, or obtaining thin (~20 μm) ground sections using a geological abrasive wheel. However, the best results were achieved with a custom-built, slow speed saw and diamond lapidary blade that cut thin (120 μm) sections. These were etched in 5% formic acid for 5 minutes, washed in running water for 1 hour and dried and mounted on perspex slides using cyanoacrylate glue. Sections were then viewed, at 8× magnification, through a binocular microscope using both transmitted polarized light and reflected light on the pencil-rubbed etched surface of the tooth.

Dentinal GLGs in all teeth were counted three times by each of two independent observers. Additionally, one observer (VGC) made a minimum of three cemental GLG counts in all teeth where the pulp was occluded, but only in a selection of teeth in which it was not. Initially, dentinal and cemental GLG counts were assessed separately, and the mean of any three counts (dentinal or cemental) that were within 15% of one another was accepted as the age of the animal. However, in teeth where counts varied by more than 15%, further counts were done until any three were within 15% of one another. Finally, for teeth where the pulp cavity was open, the mean of a combination of GLG counts in both cement and dentine was accepted as an estimate of age. Where occlusion of the pulp had occurred, only mean cemental counts were used to estimate age.

The number of dentinal and cemental GLGs in the teeth of one known-age animal ("Dolfie," PEM N6, born 30 December 1972 and died 9 August 1979) were also counted as above. In addition, because of the importance of the age estimate of this animal, a third observer (GJBR) counted GLGs in the dentine.

Results

Age and growth

More than 6½ but less than 7 dentinal GLGs were counted in teeth of the known-age animal "Dolfie" (Fig. 1). This corresponded well with the actual age of 6 years and 8 months and indicated an annual deposition of GLGs in the dentine. However, only six GLGs were counted in the cement of this animal, indicating that cemental GLGs probably reflect whole years only and may underestimate age by 1 year. Despite this, cemental and dentinal GLG counts were taken to represent age in years.

Age estimates from dentinal and cemental GLG counts of the teeth of 174 male and female *Tursiops* were well correlated ($r = 0.95$ and $r = 0.96$, respectively) up to approximately 12 GLGs; thereafter, counts diverged with increasing age due to the closure of the pulp (Fig. 2). The smallest individual from the nets was 29 kg and 125 cm, and had about 15% of the first GLG formed (2 months old). The heaviest male was 204 kg, the longest was 257 cm, and the oldest 42 years. The corresponding parameters for females were 182 kg, 249 cm, and 43 years, respectively.

The relationships of both body length and mass to age, for captured *Tursiops* and stranded or captive born neonates, were fitted to a number of growth curves, including those of Gompertz, Richards, Putter, and Schnute. However, growth with age, for both

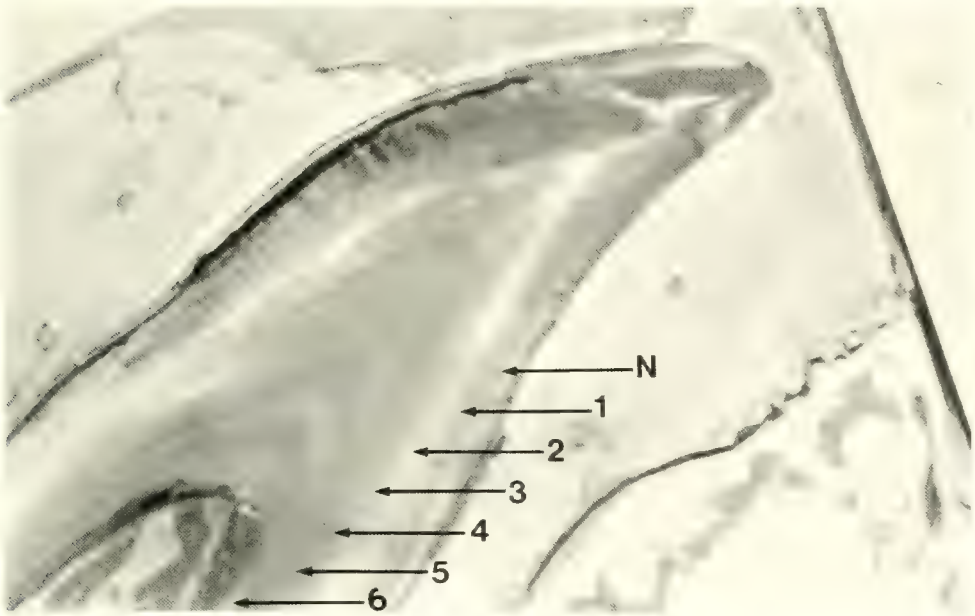

Figure 1
A thin-etched section of a tooth from "Dolfie", a captive-born bottlenose dolphin captured off southern Africa. The neonatal line (N) and the end of each of six growth-layer groups are marked.

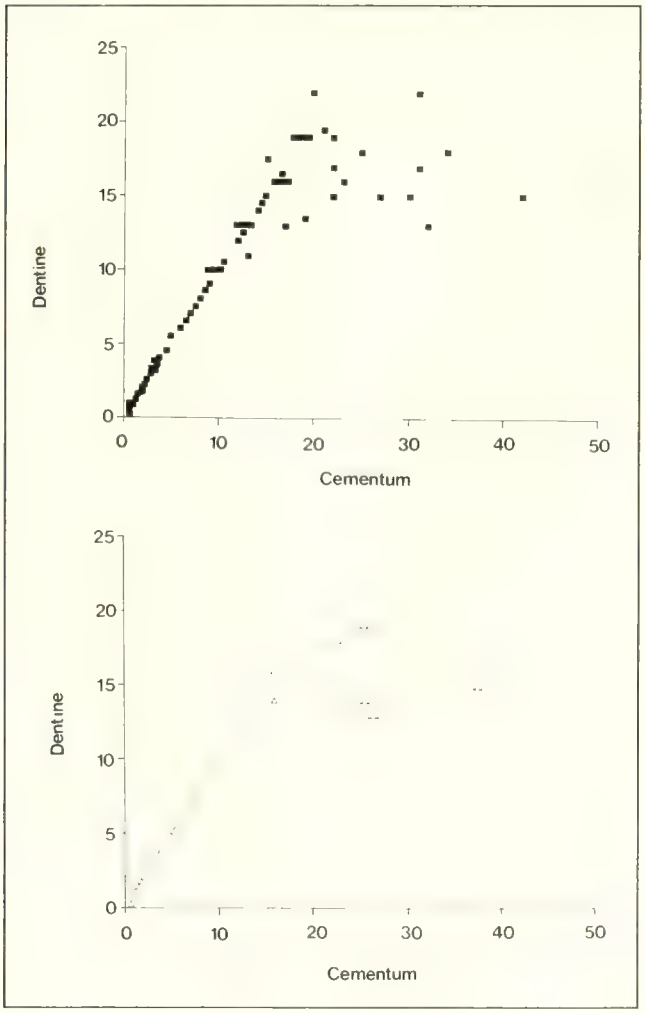

Figure 2
Relationship between growth-layer-group counts in the dentine and cement of male (■) and female (△) bottlenose dolphins captured off southern Africa.

males and females, was best defined by derived von Bertalanffy growth curves (Figs. 3,4) of the form:

$$l(t) = l_{inf}(1 - e^{-k(t-t_0)})^p$$

Asymptotic length and mass, calculated from the mean length and mass of physically mature males (243 cm and 176 kg) and females (238 cm and 160 kg), were slightly overestimated by the derived curve (Table 1), but both show that the asymptotic length and mass of males are greater than of females. There was no significant difference between the mean mass of lactating and nonlactating mature females ($t = 0.236$, $P<0.01$) which may have contributed to this sexual dimorphism.

Length and mass at birth L_{t0} predicted in Table 1 were almost identical to length and mass at birth (103 cm, range 86–115 cm, SD 7.6, $N = 26$; 13.8 kg, range 9.1–21 kg, SD 2.9, $N = 15$) calculated from the mean length and mass of captive-born or stranded neonates in which the umbilicus was unhealed.

In both males and females, most growth occurred during the first 10 to 12 years of life and thereafter reached a plateau (Figs. 3,4). In females, both mass and length increase in a smooth, continuous process with no evidence of any discontinuity. In males, length increase follows a similar pattern, whereas mass increase

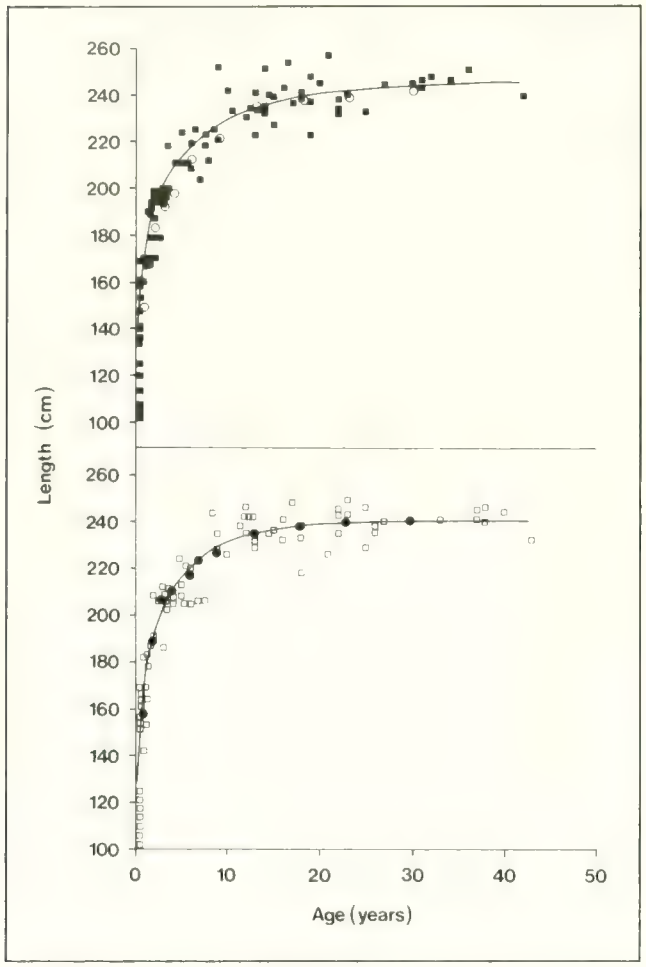

Figure 3

Increase in length with age (growth) of male (■) and female (□) bottlenose dolphins captured off southern Africa. A four-stage von Bertalanffy growth curve is fitted to these data. Mean lengths for various age classes of males (○) and females (●) are also shown.

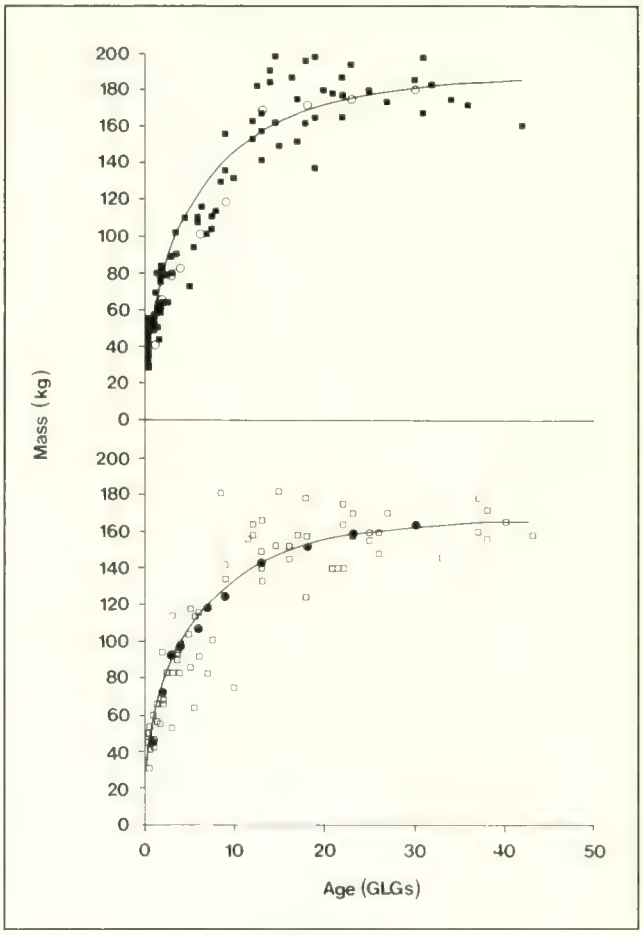

Figure 4

The increase in mass with age of male (■) and female (□) bottlenose dolphins captured off southern Africa. A four-stage von Bertalanffy growth curve is fitted to these data (see text). Mean mass for various age classes of males (○) and females (●) is also shown.

Table 1

Parameters derived from a four-stage von Bertalanffy growth curve ($L(t) = L_{inf}(1 - e^{-k(t-t_0)})^p$) fitted to age-length and age-mass data for male and female bottlenose dolphins captured off southern Africa.

	Males		Females	
Parameter	Length	Mass	Length	Mass
L_1	102.775	14.7865	102.0206	14.64186
L_2	245.016	185.217	239.9296	165.7209
t_0	−0.02261	−0.0676	−0.056844	−0.05725
L_{inf}	245.611	187.254	239.9625	166.8249
k	0.09712	0.09105	0.167249	0.099103
L_{t0}	103.4	14.9	102.3	14.8
n	100	88	88	84

L_1 = Smallest length or mass in the sample
L_2 = Largest length or mass in the sample
t_0 = Age corresponding to zero length
L_{inf} = Asymptotic length or mass
k = Constant of catabolism
p = Power constant
L_{t0} = Estimated length of mass at birth
n = Sample size

Table 2

Range in age (growth-layer-group) at which the vertebral epiphyses of male and female bottlenose dolphins captured off southern Africa were unfused, fusing, and fused.

	Unfused	Fusing	Fused
Males	0–8	4–14	>12
Females	0–6	4–13	>12

Table 3

Length, mass, and brain mass of six stranded or captive-born neonate bottlenose dolphins captured off southern Africa.

	Length (cm)	Mass (kg)	Brain mass (g)
	100	12.4	562
	105	17.7	680
	106	14.8	738
	106		595
	108	13.0	635
	109	13.4	625
Mean	106	14.3	639

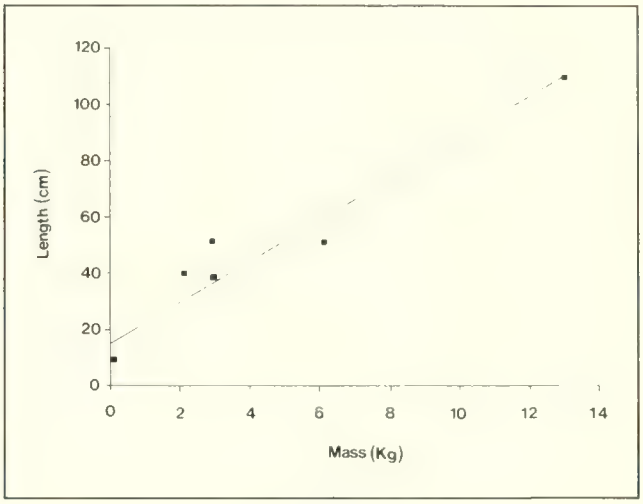

Figure 5

Fetal growth in length and mass of bottlenose dolphins captured off southern Africa, and a regression of the form (length = 23.914 + 0.006 × mass) drawn through these data.

shows a clear discontinuity between 10 and 13 years of age (Fig. 4), indicating that a two-stage growth curve may better fit these data.

The mean length and mass of the first five year-classes (calculated from calves displaying whole, completed GLGs only) showed that growth rate during the first year far exceeded that in any other. Mass increases in the first year by some 255% of mean birth mass, but increases over the subsequent 4 years slow to 49%, 13.5%, 10.6% and 3.8%, respectively. In contrast, length increase is much less rapid over this same period and is approximately 57%, 15.2%, 3.7%, 4%, and 5.5%, respectively. In both males and females the relationship between mass and length, up to asymptotic values, is well defined by power curves (males, log mass = $-5.1 + 3.06 \times$ log length, $r = 0.97$; females, log mass = $-4.7 + 2.9 \times$ log length, $r = 0.95$).

Both male and female bottlenose dolphins appear to reach physical maturity between 12 and 15 years of age (Table 2). The youngest physically mature animal was 12 years old while the oldest nonphysically mature animal was 14 years old (Table 2).

Female reproduction

Only six (2.8% of the total catch and 12% of mature females) of the captured females were pregnant, and the growth of the six fetuses—length (cm) against mass (kg)—was well defined by a linear regression (Fig. 5). Although no estimate of gestation period was possible from these data, an estimate was obtained from the relationship between neonatal and adult brain mass (Sacher and Staffeldt 1974, *in* Perrin et al. 1977). A neonatal brain mass of 639 g was estimated from the mean brain mass of six stranded or captive-born neonates in which the umbilicus was unhealed (Table 3). An asymptotic brain mass of 1460 g was calculated from the mean brain volume of physically mature females, although the variation in maximum size of females would obviously affect this. Application of the Sacher and Staffeldt equation gives a gestation period of some 372 days. An alternative method of estimating gestation period based on the relationship between birth length and gestation period (Perrin et al. 1977) yielded an estimate of 12.3 months or 374 days, assuming a birth length of 103 cm.

Birth date, to the nearest month, was back-calculated for 25 captured calves less than 1-year-old by measuring the width of deposited dentine as a proportion of the mean width of the first GLG (Fig. 6). The mean width of the first GLG layer was 279 μm ($N = 29$, range 229–331 μm) with a 95% CI of 10 μm, indicating a maximum error of about 13 days. The subtraction of age from date of capture (Fig. 6) suggests that most births occurred in summer.

In all females the majority of ovarian scars (80%) occurred in the left ovary. The maximum number of scars in any ovary was 11, with no indication that ovary mass decreased with the number of scars (Fig. 7). Age-, mass-, and length-related ovulation rates appear extremely varied in bottlenose dolphins (Fig. 8). In only one female was there one scar, so calculation of mean age at first ovulation was impossible. This 13-year-old

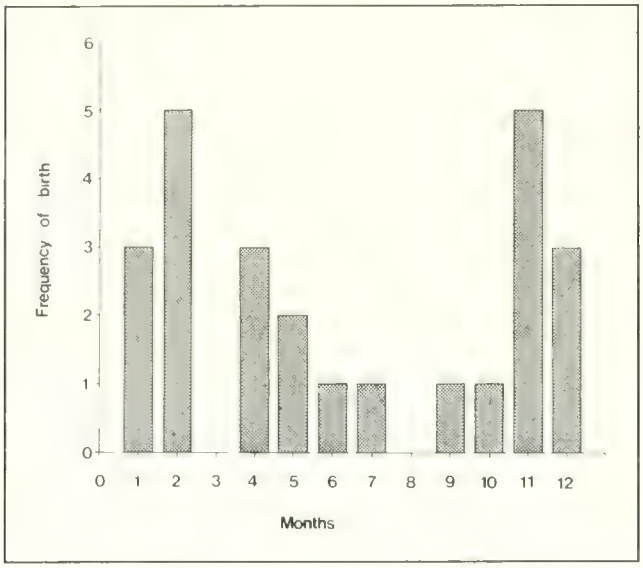

Figure 6
Birth month of 25 bottlenose dolphin calves captured off southern Africa back-calculated from the width of the first dentinal growth-layer-group.

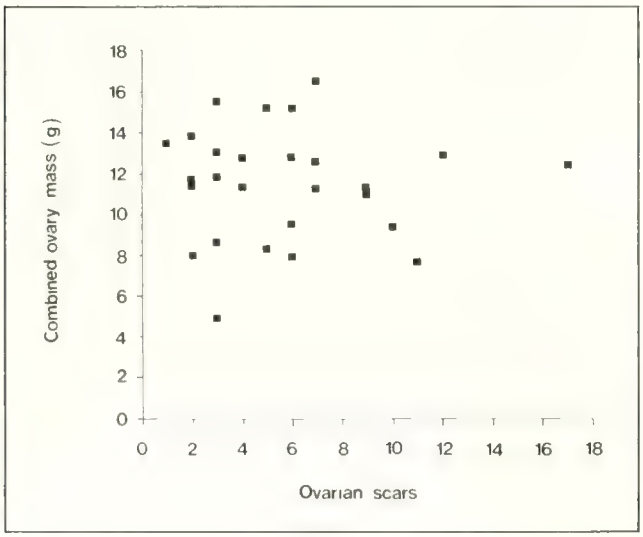

Figure 7
Relationship between combined ovary mass and the total number of ovarian scars for female bottlenose dolphins captured off southern Africa.

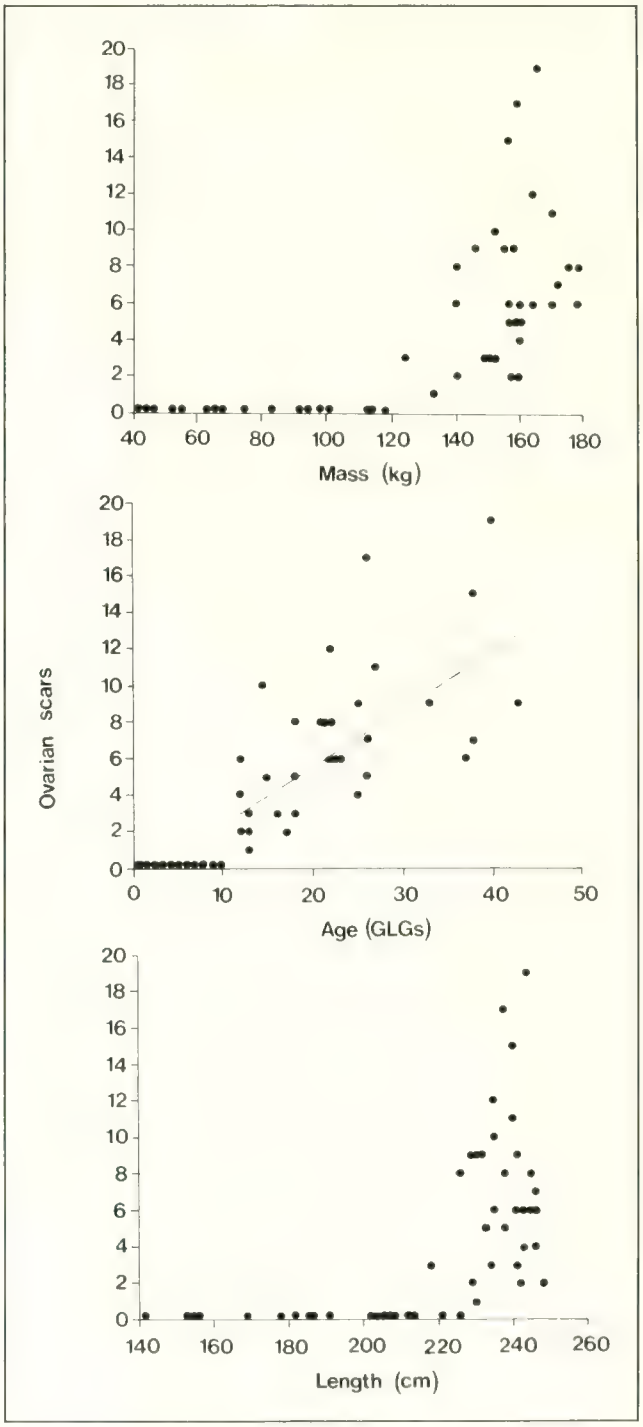

Figure 8
Increase in the number of ovarian scars with mass, age, and length of female bottlenose dolphins captured off southern Africa. A linear regression (no. ovarian scars = 0.58 − 0.29 × age) fitted to this relationship in postpubertal females is shown.

female had a *corpus albicans* measuring 10 × 8 × 8 mm (index volume 640 mm^3) and was lactating, indicating she probably had a suckling calf. Extrapolation from a regression of calf length on an index of largest corpora volume, for mother-calf pairs (Fig. 9), suggests that the calf would have been some 184 cm in length or 18 months old (Figs. 3,4), implying that her first ovulation and conception occurred at approximately 10.5 years of age.

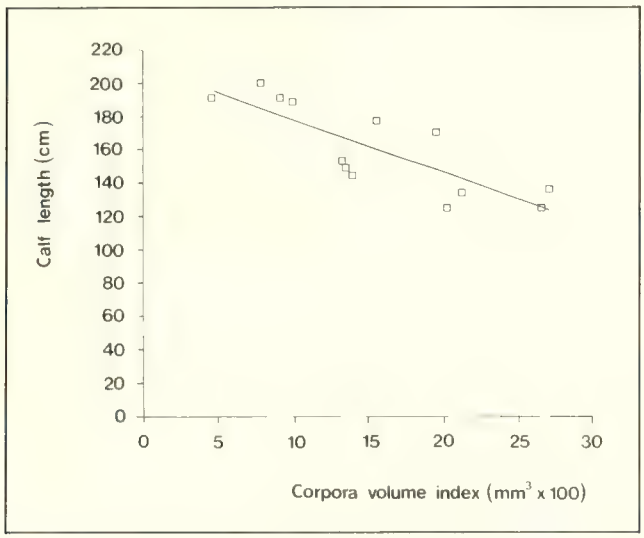

Figure 9

Relationship between the length of a bottlenose dolphin calf and an index of the volume of the most recent or largest corpus in the mother. The fit of a linear regression (calf length in cm = 209.61 − 0.032 × corpora volume index) to these data is shown.

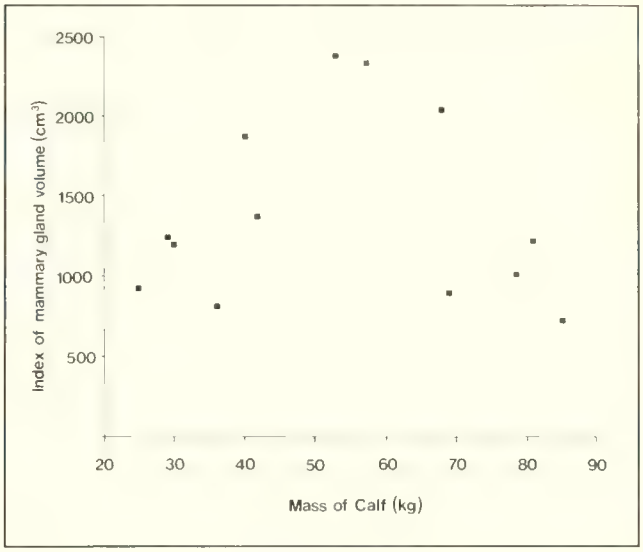

Figure 10

Relationship between the mass of a bottlenose dolphin calf and an index of the volume of the mother's mammary glands.

Two other females, 12 and 13 years old, which had each undergone two ovulations, were lactating and the index volumes of their largest *corpora albicans* were 900 mm^3 and 2100 mm^3, respectively. Extrapolation from Figure 9 suggests that the calves of these females were approximately 181 cm or 18 months old, and 143 cm or 6 months old, respectively. These data imply that at conception of the calves, these two females were about 10.5 and 9.5 years old, respectively. The above data, and the presence of 10-year-old females that had not ovulated, imply that first ovulation occurs between 9.5 and 11 years of age. One 17-year-old female had undergone two ovulations, was lactating, and had a 170-cm calf of approximately 1-year-old. This suggests that this female was 15-years-old at the time of conception of this calf, although she may have undergone a previous pregnancy.

A regression fitted to the number of ovarian scars on age of sexually mature females has a slope of 0.29 ($r = 0.6$, $N = 32$), implying that mature females, in general, ovulate at least every third year (Fig. 8). A similar regression of log of age on log of number of *corpora albicantia* was linear (log age = −0.61 + 1.03 · log # scars, $r = 0.62$), indicating no decrease in ovulation rate with age.

Length of lactation calculated from the catch statistics of animals on the Natal coast (Cockcroft and Ross In press) where 27% and 5.2% of females were lactating and pregnant, respectively, gave an estimate of 5.2 years (proportion lactating/proportion pregnant; Perrin and Reilly 1984). As this is obviously exaggerated by the overabundance of lactating females and dearth of pregnant females, alternative means of estimating lactation period are required. The relationship between calf mass and an index of mammary gland volume (length × height × depth) in 13 mother and calf pairs suggests that the mammary glands increase in size during lactation, until the calf's mass is between 60 and 70 kg, after which the mammary volume decreases (Fig. 10). Extrapolation from the growth curves suggests that calves of this mass are about 18-months-old. An examination of the stomach contents of captured calves and juveniles showed that solids first appear in stomachs at about 6 months of age, although milk remains were still evident in calves of up to 3 years of age.

Of the 20 known mother and calf pairs, ten calves were 1 year old or less, five were 1–2 years old and a further five were greater than 2 years old; the mother of one of the latter was pregnant with a fetus of only 38.5 g. Although only solids were found in the stomach of her 69-kg calf, she was still lactating, the only one of six pregnant females simultaneously lactating. These facts imply a mother and calf association of up to 3 years before a subsequent pregnancy.

Female resting period calculated from gestation period (1 year), proportion of females resting (5.3%) and the proportion of females pregnant (Perrin and Reilly 1984) yielded an estimate of about 1 year.

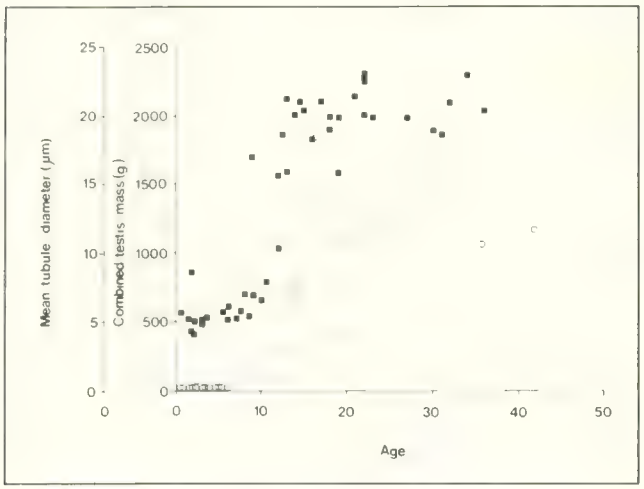

Figure 11
Increase of mean seminiferous tubule diameter (■) and combined testis mass (○) with age in male bottlenose dolphins captured off southern Africa.

Table 4
Mean age, mass, and length of male bottlenose dolphins captured off southern Africa, with testes showing no mature tubule development (stage 1), some (~half) mature tubule development (stage 2), and 75–100% of tubules mature (stage 3/4).

	Testis development stage		
	1	2	3/4
Age	4.68	14.3	20.6
Mass (kg)	90.8	151	174
Length (cm)	201	228	241
n	22	6	25

Male reproduction

No consistent differences were found between mean seminiferous tubule diameter of samples taken from the outer, middle, and inner sections of testes. In general, left and right testes were of similar mass ($r = 0.95$, $N = 46$). Combined testis mass remained low (<100 g) up to approximately 10 years of age, approximately 140 kg body mass, and a length of 225 cm, but thereafter increased rapidly (Figs. 11,12). Tubule diameter growth and state of testes development (Mitchell and Kozicki 1984) showed a similar pattern of growth with age, mass, and length (Table 4, Fig. 11), although development of tubules appeared to occur earlier than did the increase in testis mass. The maximum mature testis (stage 4) mass of any male was 1160 g and the largest apparently immature testis (stage 1) was 130 g. The smallest testis at stages 2, 3, and 4 were 140 g,

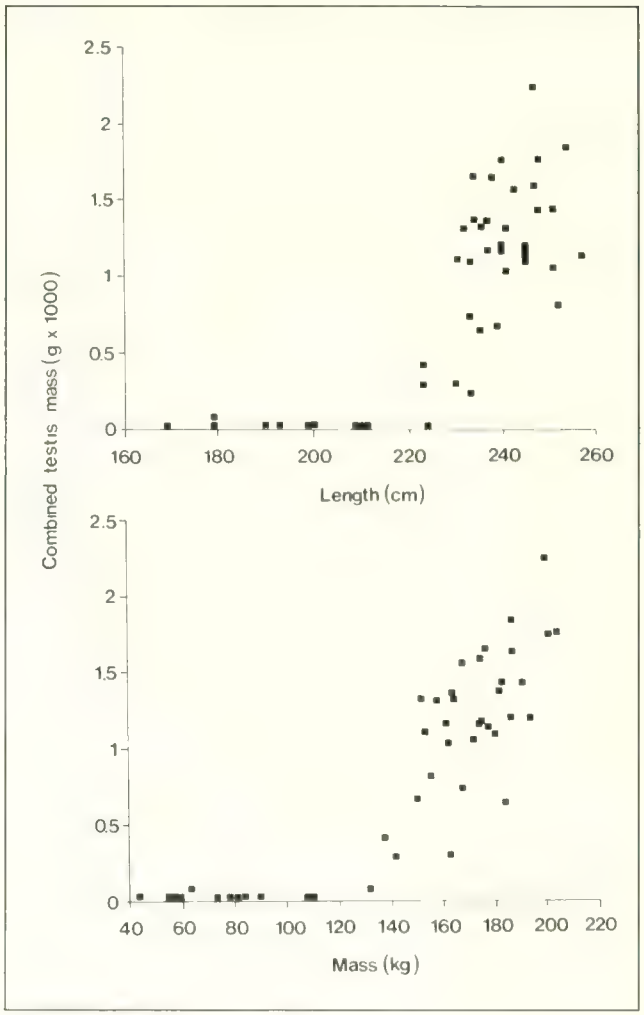

Figure 12
Increase in combined testis mass with mass and length in male bottlenose dolphins captured off southern Africa.

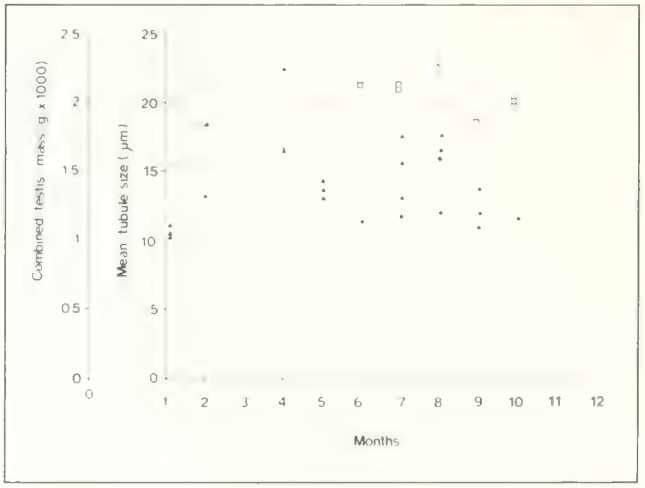

Figure 13
Influence of season (month) on combined testis mass (▲) and mean testis seminiferous tubule diameter (□) in male bottlenose dolphins captured off southern Africa.

320 g and 310 g, respectively. Mean age, mass, and length of males according to testis development stage are given in Table 4. Puberty in male *Tursiops* from the Indian Ocean may begin as early as 9 years of age but primarily between 10 and 12 years (Fig. 11). However, sexual maturity (50% each of stages 2/3 and 4) occurs only at about 14.5 years of age, a length of 240 cm and a mass of 165 kg.

There was no evidence of a seasonal pattern in either combined testis mass and tubule size (Fig. 13) or the presence of sperm in the epididymis.

Discussion

The similarity of dentinal GLG counts to "Dolfie's" actual age indicates an annual deposition of dentinal GLGs for at least the first 6 years. Ross (1984) superimposed the growth rate of this animal on a length-versus-age (dentinal GLGs) relationship in bottlenose dolphins from Natal and the Eastern Cape, and concluded that "the best fit of the points to the curve is reached when the accumulation rate of dentine layers is equal to one per year." Similarly, when the growth rate of another captive Indian Ocean animal (Cockcroft and Ross 1990b) is fitted to the curve, the relationship is best explained by an annual deposition of dentinal GLGs, also proposed for *Tursiops* in other areas (Sergeant et al. 1973, Hui 1980).

In contrast to apparently continuously deposited dentinal GLGs, cemental GLGs appear to be rapidly deposited and only accumulate as whole layers in the teeth of *Tursiops*. Nevertheless, the strong correlation between dentinal and cemental age estimates up to occlusion of the pulp cavity, and the similarity of dentinal and cemental GLG counts in teeth of the captive animal, suggest that cemental GLGs also accumulate annually and are reliable estimators of age in bottlenose dolphins from the Indian Ocean, at least up to an age of 12 years. Despite the lack of direct evidence, it seems likely that cemental GLGs are deposited annually even after 12 years.

Male and female Indian Ocean bottlenose dolphins may attain an age greater than 40 years (cf. Ross 1977) with little difference in the apparent maximum ages of the sexes. In excess of 20% of the Natal net catch were older than 20 years, indicating a long-lived species. Few data are available on the longevity of *Tursiops* elsewhere, and most existing studies have used dentinal age estimates. Sergeant et al. (1973) estimated the longevity of *Tursiops* from northeast Florida to be about 25 years, with no apparent differences in the life expectancy of males and females. Hohn (1980), in a study of *Tursiops* from the southeast coast of the United States, found animals with up to 27 dentinal GLGs, males and females reaching similar ages. In contrast, the maximum age of spotted dolphins, estimated from cemental GLGs, is in excess of 45 years (Kasuya 1976). Thus, the use of cemental GLG age estimates in future studies of bottlenose dolphins may yield greater estimates of maximum age.

The estimated mass and length at birth of Indian Ocean bottlenose dolphins in this study are comparable with those calculated by Ross (1984). Subsequent to birth, growth is rapid, particularly in terms of mass, but decreases gradually with age. The proportional length increase is similar to that previously recorded for bottlenose dolphins from Natal and the eastern Cape (Ross 1977, 1984; Cockcroft and Ross 1990b) and also those from other areas such as northeast Florida (Sergeant et al. 1973), the western North Atlantic (Hohn 1980) and captive animals from the Pacific coast of Japan (Kasuya et al. 1986). An enormous increase in mass during the first (suckling) year is well known in seals and balaenopterid whales but has not often been recorded for delphinids. Presumably, a large initial mass increase reflects the rapid development of the calf and its need to reach thermoregulatory equilibrium as well as some social and motor independence from its mother (Cockcroft and Ross 1990b) before the female's involvement with the next pregnancy and calf.

The asymptotic length and mass values obtained in this study and those of Ross (1977, 1984) are less than those for bottlenose dolphins from the western North Atlantic (Hohn 1980), Florida (Sergeant et al. 1973), and the Japanese Pacific (Kasuya et al. 1986). It is unclear why bottlenose dolphins from different areas have varying asymptotic sizes. Some authors have suggested that this may warrant the separation of the various populations to the specific level (Ross 1977), although Ross and Cockcroft (1990) have suggested that there is little morphometric evidence to suggest this and that such differences may only have resulted from environmental conditions, particularly temperature.

The asymptotic lengths of male and female Indian Ocean bottlenose dolphins are only slightly different (243 cm and 238 cm, respectively). In the western North Atlantic, Hohn (1980) found no difference in the maximum lengths of males and females. These results support the findings of Sergeant et al. (1973) that the total lengths of male and female delphinids, in general, do not appear to be different, although they found that the asymptotic length of male *Tursiops* from Florida was 20 cm greater than that of females.

In contrast, fully grown male Indian Ocean bottlenose dolphins are considerably heavier (9%) and more robust than females (176 kg and 160 kg, respectively). Lactating and nonlactating females had a similar mean mass, indicating that this mass difference cannot be

attributed to stress and blubber mass loss through lactation (Cockcroft and Ross 1990a, b). Some of this mass difference between the sexes may be a direct consequence of the male mass growth spurt between 10 and 12 years of age. It is unclear why this growth spurt is not reflected in the length of males; it may be that robusticity and not length is important in male and female interaction.

Despite this, the male growth spurt at the onset of puberty may be similar to the two-stage growth that Perrin et al. (1976, 1977) described for male and female spotted and spinner dolphins in the eastern tropical Pacific where growth showed a pubertal secondary growth spurt. In male bottlenose dolphins, this spurt occurs 4–5 years later than in spotted or spinner dolphins but also at the onset of puberty, suggesting that such growth spurts may be directly related to the attainment of sexual maturity. It is possible that this growth spurt may also be evident in female bottlenose dolphins but is not discernible owing to the small sample size.

Females mature sexually some 2 or 3 years prior to the attainment of physical maturity in contrast to males, where sexual maturity is attained just before physical maturity. In both sexes, however, physical maturity occurs almost in concert with the occlusion of the tooth pulp cavity, supporting previous suggestions that animals with occluded pulp cavities are sexually and physically mature (Ross 1977, 1984). Females attain sexual maturity at least 2 years earlier and at a lesser length and mass than do males, although the reduced number of first-time ovulators and high occurrence of females with multiple ovulations will have biased this upwards. It is not unusual for female delphinids to attain sexual maturity sometime before and at a smaller size than males. Female *Tursiops* in the western North Atlantic also appear to follow this pattern (Sergeant et al. 1973). Female spotted and spinner dolphins reach sexual maturity about 3 or 3–4 years, respectively, before males and both are smaller than their male counterparts (Perrin et al. 1976, 1977). It has been proposed that this disparity ensures more sexually mature females than males in the population (Bryden 1972). Intensive behavioral field work is needed before this suggestion can be confirmed.

Although no direct estimate of gestation period was available from the fetal growth data, both derived estimates were in excellent agreement, about 373 days. A 373-day gestation period is slightly longer than previous estimates for Indian Ocean *Tursiops*, which range from minimums of 342 and 341 days (Saayman and Tayler 1977) to maximums of 364 and 368 days (Ross 1984) in captive bottlenose dolphins. Similar estimates of the gestation period in captive *Tursiops* from other areas have been given by Tavolga and Essapian (1957), McBride and Kritzler (1951), and Kasuya (1985).

Although the sample was too small for an assessment of the age at first ovulation, the onset of ovulation in females is apparently rapid. Thereafter, there was considerable variability in the ovulation rates. Some 12- or 13-year-old females had particularly high ovulation rates, possibly a result of several initial infertile ovulations (Harrison et al. 1972). Others of the same age had low corpora counts, were all lactating, and one was pregnant, indicating that fertilization occurred on the first or second ovulation. Indirect evidence, which shows that lactational transfer of organochlorines in female bottlenose dolphins occurred after one or two ovulations (Cockcroft et al. 1989), supports the view that the majority of females conceive after one or two ovulations. The variation in ovulation rates of older females may be due, in part, to the same factors which apply to younger females and to additional reasons such as calf mortality or aborted pregnancies.

Overall, the calculated annual ovulation rate for female bottlenose dolphins was 0.28, a substantially lower rate than that observed for *Tursiops* from northeast Florida (Sergeant et al. 1973). There was little sign of reproductive senescence in females from Natal, as ovulation rate did not appear to decline with age, and there was no reduction in ovary mass with an increasing number of ovarian scars. Also, the oldest captured female was lactating, and a number of older females were captured with calves and had enlarged *corpora* in their ovaries. Results from organochlorine residue studies in these females also indicate that older females do not become senescent (Cockcroft et al. 1989). These data imply that older females do not act as "wet nurses," which is contrary to suggestions for several other species of odontocetes that manifest age-related declines in fecundity. Senescent females invest more in quality calf-rearing and a longer lactational commitment than in quantity calf-bearing, as their reproductive potential fails (Kasuya and Marsh 1984, Marsh and Kasuya 1986). However, sample numbers in this study were small and certain female-calf pairs showed an extended relationship, though there was no indication that this was restricted to older females.

Taken in combination, these facts indicate that some Indian Ocean bottlenose dolphin females are probably reproductively active until an advanced age. A similar conclusion was reached by Kasuya (*in* Marsh and Kasuya 1986) who found that although the annual pregnancy rate and the number of resting females in a sample of *Tursiops* from the Pacific declined with age, pregnant and lactating females were present in all age groups, presenting no conclusive evidence of senescence.

Although births apparently occur throughout the year, there is a peak in summer, between November and February, when over 60% of births occur. However, as birth dates were back-calculated, this may reflect the greater catch of dolphins in these months and the bias of the net catch for larger calves (Cockcroft and Ross In press), although previous work in this region noted that births occurred predominantly in late spring and summer (Ross 1977). No seasonal cycle of either testis mass, tubule diameter, or occurrence of sperm in epididymis was evident in mature males. These data also imply no distinct mating or breeding season in Indian Ocean *Tursiops*. In Florida waters, the main mating and calving season is apparently February to May (Essapian 1963), or spring to early fall (Irvine et al. 1981), which is similar to that found in the present study. In contrast, bottlenose dolphins off Argentina show a distinct summer calving and mating season (Wursig 1978). These geographical variations, however slight, indicate the adaptability of coastal *Tursiops* to local conditions.

Although it has been suggested that suckling as a nutritional source probably only lasts 1 year (Kasuya and Marsh 1984, Cockcroft and Ross 1990b), there is evidence that suckling may last at least 18 months in *Tursiops* and that non-nutritional suckling may continue for as long as 3 years for some mother and calf pairs. An estimate of the duration of lactation is difficult, where suckling extends over long periods and may serve a non-nutritional purpose such as enhancing the cow-calf bond (Brodie 1969). Of the calves from lactating female-calf pairs, 25% were over 1 year old and a further 25% were over 2 years old, and some of the latter had both milk and solids in their stomachs. The mammary glands from these lactating females, only one of which was pregnant, increased in size with calf size, until calves were at least 18 months old. In combination, these data indicate that lactation in Indian Ocean bottlenose dolphins lasts more than 1 year and in some instances may extend to more than 2 years.

This is slightly longer than previous estimates of lactation length and age at weaning based on studies of captive and captured free-ranging bottlenose dolphins (McBride and Kritzler 1951, Gurevich 1977, Saayman and Tayler 1977, Kasuya 1985, Cockcroft and Ross 1990b) and suggests a prolonged mother-calf association that may extend in free-ranging bottlenose dolphins for at least 15 months (Irvine et al. 1981). Such extended mother-calf interaction may indicate a stable school structure, such as that postulated for short-finned pilot whales off the Pacific coast of Japan, which may be indicative of late maturing, long-lived animals (Kasuya and Marsh 1984). This may equally apply to *Tursiops* where a lengthy mother-calf bond may be important in the calf's development and be a reflection of the smaller school size and inshore habitat, mastery of which may require greater maternal care and a longer learning period (Cockcroft and Ross 1990b).

During a study of captive bottlenose dolphin mother and calf association, Cockcroft and Ross (1990b) have shown that the calf's suckling rate decreased with age, although its energy requirements probably grow with its level of independence and activity. As there was no evidence of energy changes in delphinid milk during lactation (Arvy 1974) to compensate for this, the authors proposed that the quantity of milk ingested may increase as the calf's stomach volume increased (Cockcroft and Ross 1990b). This explanation is supported by the present findings that a female's mammary glands increase in size, probably increasing the volume of milk produced, during lactation.

In view of the extended lactation period of female bottlenose dolphins and the early and probably increasing intake of solid food by the calf, it is unlikely that females require a substantial interval between the end of lactation and the next pregnancy. A 1-year resting period, estimated from the catch statistics data, is almost certainly an overestimate due to catch bias. Kasuya (1985) estimated a 3-month resting period for *Tursiops* in the western north Pacific, and it is probable that Indian Ocean *Tursiops* are similar. Considering that gestation lasts about 1 year and that lactation probably lasts 18 months to 2 years, a calving interval of around 3 years can be estimated for Indian Ocean bottlenose dolphins. This estimate is in good agreement with the projected ovulation rate of one every 3 years, but assumes that all calves survive and ignores the effects of differential calf mortality (Perrin and Reilly 1984) that would lower the mean calving interval considerably.

Nothing is known of the age and sex structure of the Natal bottlenose dolphin population. The only available information is from the catch of these animals in the Natal shark nets, the sex, size, and age structure bias of which have been discussed (Cockcroft and Ross In press). Given these biases, attempts to calculate reproductive parameters from these data are flawed but provide the only means of calculating the reproductive potential of this population.

The relevant proportions in the net catch of females—mature, lactating, pregnant, and resting—are 56%, 43%, 27%, 5.2%, and 5.8%, respectively (Cockcroft and Ross In press). Annual pregnancy rates (APR; Perrin and Reilly 1984) calculated from these catch data and lactation period (either 1 or 2 years) range between 5.2% and 27%. Changes in either the proportion of females lactating or the length of lactation greatly influence this calculation, but even the highest estimate is low in comparison with values calculated for *Tursiops* in other areas; 63% in the Black Sea (Danilevsky and

Tyutyunnikov 1968, *in* Perrin and Reilly 1984) and 43.6% and 40.4% for the western north Pacific (Kasuya and Izumisawa 1981, *in* Perrin and Reilly 1984; Kasuya 1985).

Gross annual reproduction rate (GARR) (Perrin and Reilly 1984) calculated from catch statistics and the range of APR values yields estimates between 0.043 and 0.065. Although biases in the catch will influence these GARR estimates, they are useful for comparative purposes. The former GARR estimate is greater than that calculated for an unexploited stock of *Tursiops* from eastern Australian waters, although this was based on an unreliable technique of estimating calf numbers from aerial surveys (Lear and Bryden 1980, *in* Perrin and Reilly 1984). The latter GARR figure, although probably an overestimate, is some 40% and 500% lower than those estimated for exploited populations of *Tursiops* off Iki Island, Japan (Kasuya 1985) and in the Black Sea (Danilevsky and Tyutyunnikov 1968, *in* Perrin and Reilly 1984), respectively.

The probable biases in the calculated APR and GARR estimates suggest that an assessment of the theoretical maximum natural rate of increase (ROI) of the Natal bottlenose dolphin population would be more practical. Assuming a calving interval of 2–3 years, age at first breeding of 10 years, and an annual survival rate of less than 0.97, an ROI of 4–6% can be calculated (Reilly and Barlow 1986). The ROI makes allowances for adult and calf mortality not accounted for by a GARR estimate, which, therefore, infers that even the greater GARR figure may be an underestimate. Given an annual increase of as much as 6% of the estimated 900 population, the mean annual mortality of bottlenose dolphins in shark nets—32 dolphins per year including about 4 reproductive females—in conjunction with whatever other sources of man-induced mortality, such as the probable death of first-born neonates through pollutant toxicity (Cockcroft et al. 1989), implies that mortalities may be close to or exceed the likely replacement rate of this population. However, this conclusion should be viewed with some caution, as it is based on an estimated population of only some 900 dolphins, although biases of aerial counts suggest that numbers may be greater (Cockcroft et al. In press). Additionally, other factors may also influence understanding of the reproductive capacity of this population. If bottlenose dolphins on the Natal coast are geographically separated for long periods (Cockcroft et al. 1989) with little mixing even of adjacent groups (Cockcroft et al. In press), then reproductive parameters for females in different areas may vary and have a profound effect on calculated replacement potentials.

The incidental mortality and probable depletion of long-lived dolphins, that invest many years in the care and socialization of their young and are resident in areas with which they are familiar, is of concern. The future management of the Natal bottlenose dolphin population requires accurate population figures and an unbiased estimate of age and sex structure. Regular aerial, boat, and shore-based surveys along the Natal coast are needed to define the former. The latter is best obtained through a combination of intensive field observational work on free-ranging dolphins and a continued monitoring of captured animals.

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Oceanic Dispersion of Larval Fish and its Implication for Mortality Estimates: Case Study of Walleye Pollock Larvae in Shelikof Strait, Alaska

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Abstract.–To estimate mortality and abundance of walleye pollock *Theragra chalcogramma* larvae in Shelikof Strait, Alaska, during spring 1981, a diffusion-advection model, combined with growth and death of fish larvae, was applied. Physical parameters (diffusion coefficients and advection rates) were derived from the distributional variances and centroids of fish larvae collected in ichthyoplankton surveys. The diffusion coefficient and the advection rate in the along-strait direction were 65.2 km^2/day and 2.7–4.2 km/day, respectively, which compared favorably with values obtained from moored current-meter data. Simulation revealed that the expected distribution of larvae was similar to that observed from ichthyoplankton samplings, and that around 20% of the larvae drifted out of the survey area in Shelikof Strait within the 1-month sampling period. The larval fraction dispersed out of the survey area was used to revise larval mortality and abundance estimates. Revised mortality (0.070/day) was close to that (0.063/day) determined from examining larval patches. The simulation in this paper resulted in an increase by a factor of 1.5 in the estimated total larval abundance compared with earlier estimates and field observations.

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Most marine fish have a period of planktonic existence during egg and larval stages. Since early in this century it has been believed that survival during early life determines year-class strength and recruitment variability to fisheries (Hjort 1914). Furthermore, recruitment processes are quite complex because the biological and environmental factors which act on eggs and larvae are closely related (Wooster et al. 1983). Hence, the relationship between organisms and their environment is critical for understanding recruitment variability. The observed patterns of egg and larval distributions can be considered to be the result of a combination of fundamental processes, including spawning time and location, advection, diffusion, growth and mortality. These parameters could be identified using biological data.

The early-life stages of walleye pollock *Theragra chalcogramma* whose biomass is the largest of a single species in world fisheries (Sharp 1987), have been the objects of considerable research in recent years. In Shelikof Strait (Fig. 1), about 90% of the eggs were produced between 25 March and 15 April 1981, and they have approximately a 2-week embryonic period at 5°C (Kim 1989). Spawning produces a patch of planktonic eggs and larvae that can be followed as they develop and are advected in prevailing currents toward the southwest. In Shelikof Strait walleye pollock eggs exist at depths below 150 m due to their high specific gravity. Their transport rate from the spawning area is very small because of weak circulation in deep water (Kendall and Kim 1989).

Eggs of late developmental stage would move upward fast due to the decreased specific gravity of old eggs, and the eggs hatch mid-depth in the water column (Kim 1987). Also the specific gravity of newly hatched larvae is continuously decreasing, so that most larvae are found within the upper 60 m of the surface (Kendall et al. 1987). Kim and Kendall (1989) described the distribution and transport pattern of larvae in Shelikof Strait during spring. Young larvae occupy a relatively small area and form a dense patch, while older larvae spread over a broader area in Shelikof Strait, showing the importance of diffusion on the larval patch. These larval patches have been identified for at

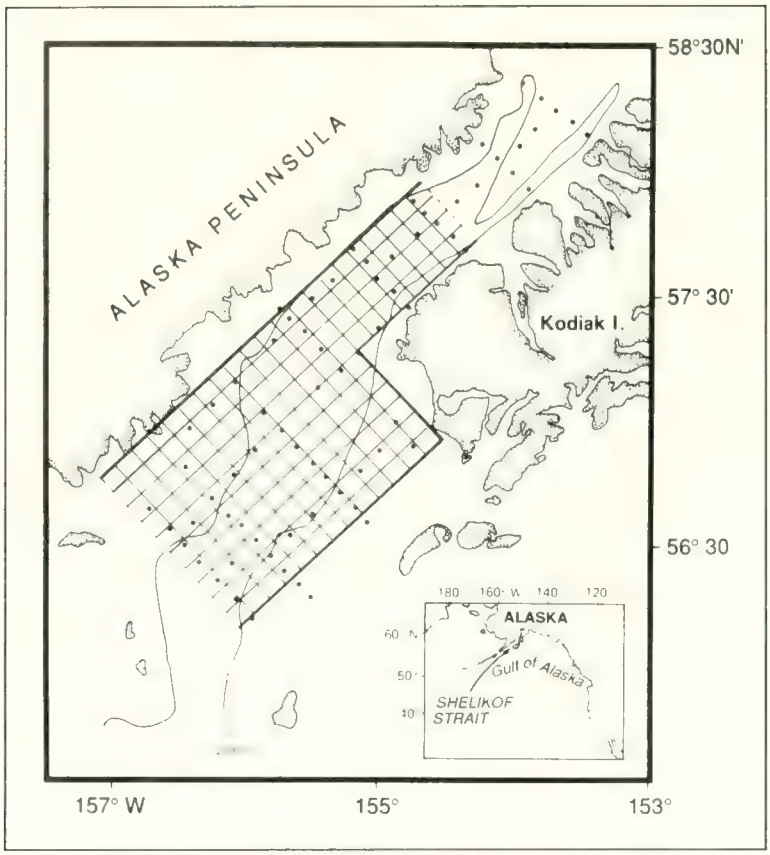

Figure 1
Typical locations of sampling stations (•) and the grid pattern used for the computer simulation. The flux of larvae through the solid lines is zero. The dashed lines are open boundaries of the model that permit the loss of larvae.

least a month after hatching (Incze et al. 1989). Assuming no drift or dispersion of larvae away from the sampling area, the instantaneous daily mortality was estimated as 0.086 (Kim and Gunderson 1989). The effects of advection and diffusion on the larval mass, however, can cause errors in estimation of mortality and abundance. Hence, the distribution and abundance of walleye pollock larvae in Shelikof Strait should be reconsidered in the light of oceanic diffusion-advection theory (McGurk 1989).

The main objectives of this paper are:

1 Estimation of diffusion coefficients and advection rates of walleye pollock larvae based on ichthyoplankton distribution in Shelikof Strait;

2 Description of expected larval distribution and abundance with time from a computer simulation using a diffusion-advection model; and

3 Reestimation of larval mortality and expected larval abundance reported in Kim and Gunderson (1989) and comparison of these results with field observations.

Background of theories and model

In general, the simplest approach to the diffusion problem for particles in a fluid medium follows from the assumption that the rate of diffusion is directly proportional to the local concentration gradient (Okubo 1980). Walleye pollock larvae in Shelikof Strait are advected and diffused in the upper 60 m during early larval stages (Kendall et al. 1987), and the swimming ability of larvae less than 10 mm is assumed to be inconsequential. Therefore, a horizontal two-dimensional diffusion-advection model is applicable to changes in the distribution and abundance of young walleye pollock larvae in Shelikof Strait. Current speeds (u and v) and diffusion coefficients (K_x and K_y) are set constant, with the assumption of a homogeneous turbulence field and negligible horizontal divergence. Newly hatched larvae (i.e., the source material in the diffusion-advection model) are assumed to be produced daily at a fixed location near the center of Shelikof Strait (Kim and Kendall 1989). Once larvae that dispersed from the source point arrived at the Alaska Peninsula coast, they were required to remain there, since the shallow coastal region is considered a nursery area of young fish (Walters et al. 1985). Since larvae grow as they drift, the simulated distribution and abundance of larvae can be divided into several size groups. The partial differential equation, with initial condition $C_i(x, y, T_1) = 0$ and boundary conditions as described above, is

$$\frac{\partial C_i}{\partial t} = K_x \frac{\partial^2 C_i}{\partial x^2} + K_y \frac{\partial^2 C_i}{\partial y^2} - u \frac{\partial C_i}{\partial x} - v \frac{\partial C_i}{\partial y} - rC_i \qquad (1)$$

where C_i = larval concentration of i-th cohort (number/m^2),
x and y = along- and cross-strait coordinates,
K_x and K_y = along- and cross-strait turbulence diffusion coefficients,
u and v = along- and cross-strait velocity components,
r = instantaneous daily mortality of larvae, and
T_1 = starting time of i-th cohort larval production.

The solution using Laplace transform is

$$C_i(x,y,t) = \frac{1}{4\pi\sqrt{K_x K_y}} \int_{T_1}^{t} \frac{P_i(T)}{(t-T)} e^{r(t-T)} \left\{\sum_a e^{-\frac{(x-A_a)^2}{4K_x(t-T)}}\right\}\left\{\sum_b e^{-\frac{(y-B_b)^2}{4K_y(t-T)}}\right\} dT \qquad (2)$$

where $C_i(x,y,t)$ = larval concentration of i-th cohort at time t at point (x,y),
$P_i(T)$ = i-th cohort's larval production rate at time T ($T_1<T<t$) and at source point (x_0, y_0).

$$A_a = (-1)^{|a|} X^* + a(x_{+L} - x_{-L}) + \mathrm{mod}(|a|,2)(x_{+L} + x_{-L})$$

$$B_b = (-1)^{|b|} Y^* + b(y_{+L} - y_{-L}) + \mathrm{mod}(|b|,2)(y_{+L} + y_{-L})$$

where a and b = indices of symbol summation (Σ)
if there is no boundary, a or b = 0
if there is negative-side ($-L$) boundary only, $a = -1, 0$; $b = -1, 0$
if there is positive-side ($+L$) boundary only, $a = 0, 1$; $b = 0, 1$,
if there are boundaries at both sides, $a = -\infty, \ldots, 0, \ldots, +\infty$; $b = -\infty, \ldots, 0, \ldots, +\infty$

$X^* = x_0 + u(t-T)$
$Y^* = y_0 + v(t-T)$

x_{+L}, x_{-L}, y_{+L}, and y_{-L} = positive and negative side boundaries in x and y coordinates,
mod($|a|$,2) = remainder of $|a|$ divided by 2, and
mod($|b|$,2) = remainder of $|b|$ divided by 2.

The area of Shelikof Strait used in the computer simulation was divided into 162 10×10 km grid areas with boundaries along the Alaska Peninsula and Kodiak Island (Fig. 1). The grid scheme was used to obtain contour patterns of results and to compare the simulated values with observations. To obtain larval abundance for each grid area from Equation (2), numerical integration was used, since the integration could not be handled by further analytic approach. For time integration, an 8-point Gaussian Quadrature is used (Scheid 1968), and for spatial integration an error-function infinite series is used (Gradshteyn and Ryzhik 1980).

Once all parameters were selected for the diffusion-advection equation, the simulation program was run for 50 days starting on 5 April (Julian day 95) and continuing until 24 May (Julian day 144). Larvae were produced near the central strait every day. They then were advected and diffused in the grid area according to given values of the parameters. Finally the concentration obtained from the model for each size group during the 5-day period of 20–24 May was averaged to show the expected larval abundance of each size group in late May 1981.

The mortality parameter in Equations (1) and (2) was derived in Kim and Gunderson (1989) from observed data during two consecutive surveys (i.e., 26–30 April and 20–24 May, 1981) assuming that larvae stayed in the survey area and that the larval population decreased exponentially with time. If, however, some of the larval cohort that existed in the sampling area during the first survey drifted out of the area by the second survey (called out-fraction in this paper), then the mortality rate must be an overestimate. The out-fraction of larval abundance—which is the ratio of the larval abundance evicted from the simulation box in Figure 1 to the total larval abundance assuming no dispersion—is computed after simulation, and this computation can be used to estimate a new mortality value in an exponentially decreasing population with time:

$$Z^*(L) = -\frac{1}{\Delta T} \ln\left\{\frac{d_2/(1-f)}{d_1}\right\} = -\frac{1}{\Delta T} \ln\left\{\frac{d_2}{d_1}\right\} + \frac{1}{\Delta T} \ln(1-f) \qquad (3)$$

where $Z^*(L)$ = revised instantaneous daily larval mortality,
ΔT = time difference in days (24 days) between surveys,

d_1 and d_2 = observed larval densities during late April and late May surveys, respectively, and
f = out-fraction.

Note that the first term of the right side means the daily mortality rate for the closed population, which was used in Kim and Gunderson (1989), and that the second term is the correction factor due to dispersion. Once the new mortality rate was determined, it was used for the second simulation to obtain a revised estimate of larval abundance in late May 1981.

Parameter estimation

Some parameters for the model were available from other studies. Kim and Gunderson (1989) found two dominant larval cohorts during April and May surveys, and assumed that 4–5 mm larvae in late April had grown to 8–9 mm, and regarded this group as cohort 1. Also, the 5–6 mm size class in late April and the 9–10 mm size class in late May were treated as cohort 2. By comparing the larval abundances of these two cohorts, they estimated an instantaneous daily larval mortality of 0.086 and a daily growth rate of 0.17 mm.

Daily larval production was derived from daily egg production and time-specific egg mortality during development (Kim and Gunderson 1989). A rapid increase in daily larval production occurred in mid-April, and most larvae were produced during late April (Table 1). Toward the end of the spawning season, larval production decreased but tended to be prolonged due to decreased egg mortality late in the spawning season.

Advective velocities and turbulent diffusivities were derived by examining changes in the distributional centroids and variances of several larval size groups. We treated the distribution of a certain size of larvae at a specific time as a single dispersing system in Shelikof Strait. The change in the centroids in along- and cross-strait coordinates for three size groups (4–5, 5–6, and 6–7 mm) from each survey was used to estimate advection, assumming that larvae were hatched in the same area and that these larvae were not flushed out of

Table 1

Estimates of daily larval production of walleye pollock after 14-day incubation period in Shelikof Strait during spring 1981, using estimated daily egg production and time-specific egg mortality in Kim and Gunderson (1989). Dates 95 and 144 denote 5 April and 24 May, respectively.

Date of year	Daily larval production ($\times 10^9$)	Date of year	Daily larval production ($\times 10^9$)
95	23	120	1103
96	48	121	1027
97	77	122	938
98	111	123	835
99	151	124	717
100	197	125	584
101	250	126	435
102	311	127	270
103	380	128	37
104	458	129	38
105	546	130	37
106	1016	131	38
107	1557	132	38
108	2174	133	39
109	2873	134	39
110	3087	135	38
111	3311	136	38
112	3545	137	38
113	3790	138	37
114	3294	139	37
115	2711	140	36
116	2034	141	35
117	1257	142	34
118	1217	143	33
119	1166	144	32

Table 2

Comparison of walleye pollock larval mortality rates, advection rates, and diffusion coefficients in Shelikof Strait during spring 1981.

	Instantaneous daily mortality	Advection rate (km/day) u April	u May	v April	v May	Diffusion coefficients (km^2/day) K_x	K_y
This paper	0.070	4.2	2.7	1.3	0.4	65.2	3.6
Reed et al. (1989)	0.063	4.3				43.2	

Shelikof Strait. Estimates of u and v, from regression analysis (see Table 1 in Kim and Kendall (1988) for data) were 4.2 and 1.3 km/day in April, and 2.7 and 0.4 km/day in May, respectively (Table 2). Because the variance of the horizontal distribution is a suitable measure of the spread of the substance (Bowden 1983, Okubo 1971), the change in variance (i.e., S_x^2 and S_y^2 for along- and cross-strait directions) with time provides a reasonable measure of the diffusion coefficient;

$$K_x = \frac{1}{2}\frac{dS_x^2}{dt} \cong \frac{S_{x,t1}^2 - S_{x,t0}^2}{2\Delta t} \quad (4)$$

$$K_y = \frac{1}{2}\frac{dS_y^2}{dt} \cong \frac{S_{y,t1}^2 - S_{y,t0}^2}{2\Delta t} \quad (5)$$

where $S_{x,t0}^2$, $S_{x,t1}^2$, $S_{y,t0}^2$, and $S_{y,t1}^2$ are the spatial variances at time $t0$ and time $t1$ in along- and cross-strait directions, and $\Delta t = t1 - t0$. The variances of two dominant larval cohorts were calculated as in Kim (1987). Variances of larval distribution were much increased in a month, and along-strait components were dominant compared with those in the cross-strait direction (Table 3). The estimated K_x for these two cohorts were 79.6 and 50.7 km^2/day (average 65.2). For K_y, the values were 1.0 and 6.3 km^2/day (average 3.6) (Table 2).

Table 3

Spatial variances of larval distributions of two major cohorts of walleye pollock larvae in Shelikof Strait during late April and late May 1981. The larval sizes of cohorts 1 and 2 in late April are 4–5 mm and 5–6 mm, and they grow to 8–9 mm and 9–10 mm in late May, respectively.

		Variance (km^2)	
		late April	late May
Cohort 1	S_x^2	1292	5114
	S_y^2	563	609
Cohort 2	S_x^2	3066	5500
	S_y^2	302	606

Simulation results

Spatial distribution and abundance of larvae

The model distribution of larvae in late May after 50 days of simulation was similar to that observed. Two major larval cohorts, 8–9 mm and 9–10 mm size groups, were selected for comparing the model and observed distributions (Fig. 2). In general, the simulated centroids of distribution were close to the densest patches of the larvae, and the area of larval distribution and contour levels of the larval concentrations were not very different from those observed. The simulation demonstrated the elliptical pattern of distribution, which was elongated in the along-strait direction, and the southwesterly movement of centroids from the main hatching area. The first (8–9 mm) and second (9–10 mm) cohorts drifted 92 km and 114 km, respectively, from the source point after hatching.

The maximum size of larvae was 12 mm, and the abundance of larvae and the out-fraction in each size group were computed. Comparing the simulated values with the observed ones, we found that the results were very close (Table 4). Also, as expected, the effect of out-fraction on larval distribution was more important for the larger size group than the smaller group. This was caused by the larger larval size having a higher out-fraction value. Negligible amounts of small larvae were advected from the simulation box, but over 50% of the large larvae were removed. Among total larval abundance, about 20% were flushed out of the simulation area. This concept of out-fraction due to diffusion and advection might change the larval abundance and mortality previously reported by Kim and Gunderson (1989). Even though their derived estimates agreed well with observed ones, their results should be reconsidered because the areas involved for abundance estimates were not the same. Our study revealed that their sampling area, which was similar to our simulation box, was only part of the area of larval occurrence in Shelikof Strait. Therefore the total larval abundance should be higher than they observed, and the simulated abundance within the simulation box should be close to that observed. In Table 4, the reason for the smaller larval abundance in the simulation box (3.37×10^{12}) than observed (4.15×10^{12}) might be due to their overestimate of the mortality rate.

Re-estimation of larval mortality and abundance

The first approximation of larval mortality has been recalculated using the out-fraction in Table 4. By applying the out-fractions of the two major cohorts to Equation (3), we computed revised instantaneous daily mortalities of 0.081 and 0.059 from the first and second cohorts, respectively (average 0.070). Assuming no significant change in diffusion coefficients, the revised mortality rate was used for the second computer simulation of the diffusion-advection model. Figure 3 revealed that the second simulation resulted in a 50% increase in the total larval abundance (6.21×10^{12}) in Shelikof Strait, compared with the first simulation (4.23×10^{12} from Table 4). The size-specific abundance

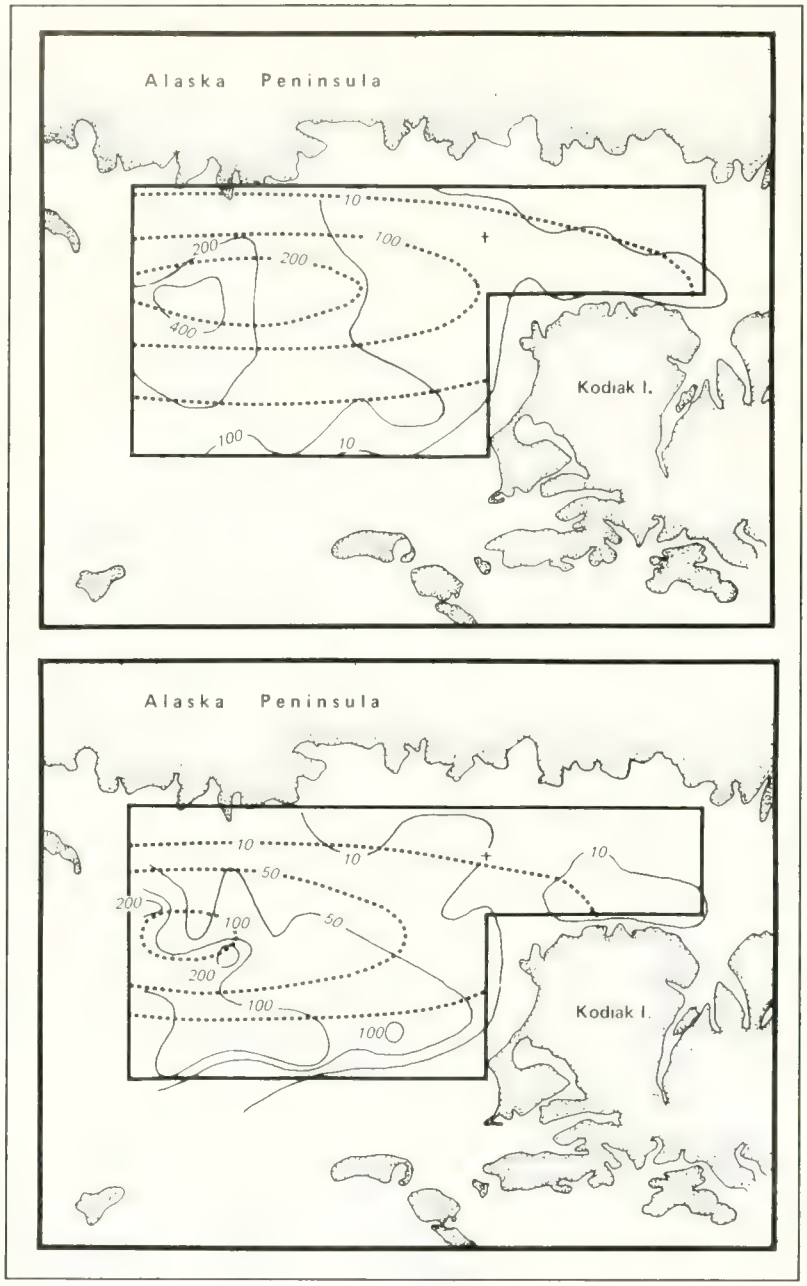

Figure 2
Contours of observed (———) and estimated (---) distributions of (a) 8–9 mm and (b) 9–10 mm walleye pollock larvae during late May 1981. Source points of larvae are indicated by (+) in each map.

of larvae within the simulation box was compared with the observed values, because the area used in the simulation could be regarded as the survey area. In general, the trends in size abundance curves, as well as the absolute abundances, were very similar to one another. The abundance of two major cohorts, both observed and simulated, consisted of about 50% of the total abundance.

Discussion

The application of a diffusion-advection model to examine the dispersal of larvae helps not only to explain spatiotemporal distribution of abundance but also to revise estimates of population parameters such as larval mortality. Difficulties in determining parameter values, however, often arise in this kind of study. In describing plankton distribution, the physical properties (diffusion coefficients and advection rates) often

Table 4

Simulated abundances of walleye pollock larvae in Shelikof Strait during late May 1981 resulted from the first computer simulation, using a daily instantaneous mortality rate of 0.086 and observed values derived from Kim (1987).

Larval size (mm)	Simulated larval abundance ($\times 10^{12}$)		Out-fraction	Observed larval abundance ($\times 10^{12}$)
	Total	Simulation box		
<4	0.033	0.033	0.0000	0.004
4–5	0.157	0.157	0.0006	0.057
5–6	0.112	0.111	0.0128	0.111
6–7	0.627	0.593	0.0538	0.496
7–8	1.011	0.881	0.1281	1.221
8–9	1.509	1.120	0.2576	1.350
9–10	0.701	0.436	0.3786	0.627
10–11	0.073	0.035	0.5200	0.204
11–12	0.008	0.003	0.6367	0.058
Total	4.230	3.369	0.2036	4.149

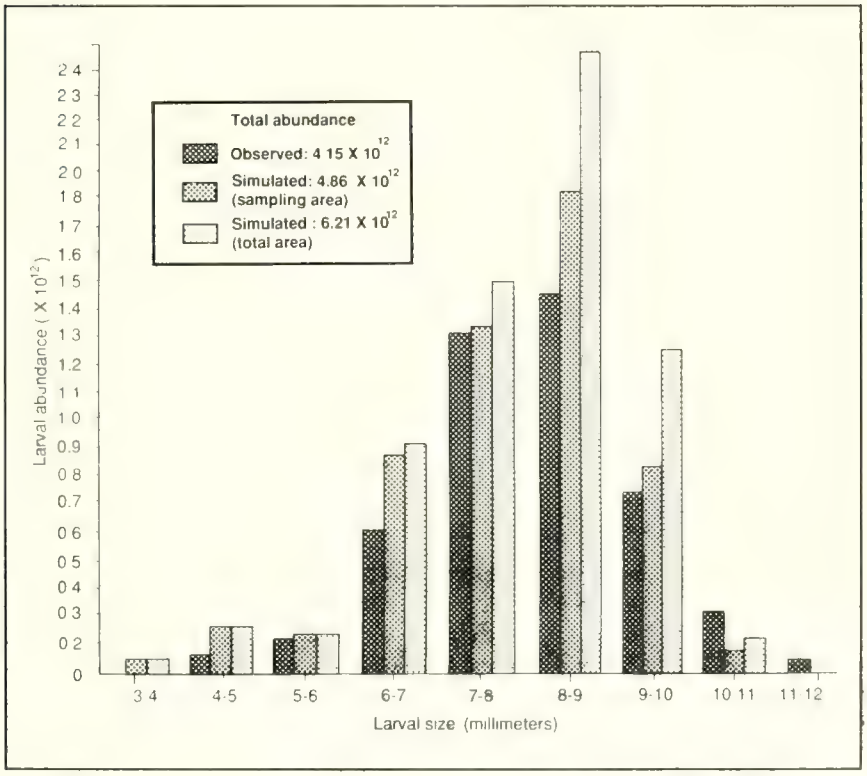

Figure 3

Simulated larval abundance from the second computer simulation using a revised mortality rate of 0.070/day, and observed larval abundance in Table 3. Notice the difference in the simulated abundances from the sampling area and the total area.

are calculated from oceanic current data, wind speed, temperature distribution, or results of dye experiments (Talbot 1974, Talbot 1977, Power and McCleave 1983, Sundby 1983), even though they do not represent the actual diffusion and advection of dispersing organisms. The collection of diffusion coefficients and advection rates from several sources is very important to understand the characteristics of the oceanic situation. Aside from measuring the dispersion using inert tracers, the use of plankton sampling data to derive these parameters has been limited because of the complexity of biological systems in the sea. The mobility and mortality of larvae may bias in estimating such parameters. The emphasis of this paper is how biological sampling data can be used for estimating physical properties, when the swimming ability of the larvae is not significant.

Reed et al. (1989) estimated parameters based on current measurement and larval patch in Shelikof Strait. By examining the abundance in small areas around the densest larval patches found in April and May surveys, they estimated an instantaneous mortality rate of 0.063/day and an advection rate of 4.3 km/day (Table 2), which are in excellent agreement with our estimates. Also, the estimation of eddy diffusivity in the along-strait direction of 43.2 km^2/day by Reed et al. (1989) did not differ greatly from our mean value of 65.2 km^2 (Table 2), even though the former was derived from moored current meter data in the surface layer (56 m) and the latter from larval distribution. These estimates are realistic only in a mean sense, because they vary in both time and space.

The diffusion process tends to destroy larval aggregation until larvae reach a certain size, so that patchiness will decrease with time. The Lloyd Patchiness Index (LPI) has been frequently used for describing aggregations of organisms (Lloyd 1967), and Kim (1987) discussed changes in LPI of walleye pollock larvae as they grew. The smaller size groups of larvae usually had a higher LPI, but it decreased until a size of about 10 mm because of dispersal of the larval patch. For sizes greater than 10 mm, although their contribution to the total larval abundance was very small, the LPI increased with length, perhaps because of reaggregation of the larvae as their swimming ability increased. If a larval retention mechanism worked for large larvae (10–12 mm) in Shelikof Strait due to increased swimming ability, that might explain the higher larval abundance from field samplings than that from the simulation shown in Figure 3. Similar examples of larval aggregation (i.e., initially patchy, dispersing until a larval size of around 10 mm, and then patchy again) were reported for northern anchovy and jack mackerel off California (Hewitt 1982).

The expected total larval abundance from the first simulation was almost identical to that in Kim and Gunderson (1989) because the same parameter values were used. By adding the concept of diffusion and advection to their model, elaborations on mortality and expected abundance of walleye pollock larvae were made. Based upon good agreement between observed and simulated results, this paper has emphasized that dispersion (or emigration) of organisms is important in the field of population dynamics.

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Tag Shedding by Southern Bluefin Tuna *Thunnus maccoyii*

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Abstract.—Models are formulated for estimating tag-shedding rates from recapture records for eight double-tagging experiments with southern bluefin tuna (*Thunnus maccoyii*) in three Australian fishing areas. These models incorporate either a constant or time-varying rate of tag shedding and allow for the possibility of immediate tag shedding. Likelihood ratio tests are used to select the most parsimonious model for each data set. The probability of a tag being shed after 4 years at liberty (the length of the most recent experiments) varied from around 0.2 for the 1983 and 1984 experiments to 0.5–0.7 for the experiments carried out in the 1960s and 1970s. Although a single, best-fitting model was selected in all but one experiment and despite the large total numbers of recoveries, precise estimates of long-term shedding rates could not be obtained because there were relatively few long-term data. This has significant implications for analyses of tag-return data that give heavy weighting to long-term recaptures.

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Southern bluefin tuna *Thunnus maccoyii* were tagged throughout the 1960s in three areas of major Australian commercial fishing activity: off the south coast of Western Australia (WA), in the Great Australian Bight off South Australia (SA), and off the south coast of New South Wales (NSW). During the 1970s, tagging took place mainly off WA. The aim of these experiments was to provide information on movements, growth, and mortality of the southern bluefin. In 1983 and 1984, new experiments were initiated off WA and SA in order to answer more specific questions relating to fishery interactions, yield-per-recruit, and schooling behavior, as well as to update information obtained from the previous experiments (Majkowski and Murphy 1983). Apart from the period prior to 1963, almost all fish were double tagged.

Quantitative analyses of tagging data that require an estimate of the total number of recaptures of tagged fish (e.g., fishery interactions, yield-per-recruit, and mortality) need to take account of tag loss due to shedding. As reviewed by Wetherall (1982), this problem can be approached in two ways. If estimation of mortality rates is the main objective of the analysis, one can attempt to model the entire process of removal of tags from the population directly by incorporating into the model parameters that account for all sources of removal, i.e., natural mortality, fishing mortality, permanent emigration, nonreporting of recaptured tags, and tag shedding. Alternatively, tag-shedding rates may be estimated independently from a double-tagging experiment and the recovery data adjusted accordingly before proceeding with further analyses (other losses, e.g., non-reporting, may also require independent estimation). A disadvantage of the former approach is that, even if simple functions are chosen to describe mortality, emigration, and tag shedding, the model will inevitably be parameter-laden, and therefore difficult to estimate. In any case, such models will not necessarily lend themselves to analyses of interactions and yields-per-recruit, where the mortality and emigration processes are embedded in the recapture statistics and do not necessarily require explicit resolution (Majkowski et al. 1984).

The aim of this paper is to estimate tag-shedding rates for a number of southern bluefin tuna double-tagging experiments, with a view to using these estimates as the basis for correcting for tag shedding in other analyses. Hynd (1969) made a preliminary estimate of the tag-shedding rate, assumed constant, based on recoveries up to 1968 only. Subsequently, Kirkwood (1981) developed generalized tag-shedding models and analyzed recoveries of southern bluefin tuna that were double tagged during the period 1962–76 but excluded all tagging that was contracted to fishermen. In both cases, these analyses used tag-recovery data that were grouped by time of recovery. A reevaluation of southern bluefin tuna tag shedding is now appropriate because, (1) for a number of present

Table 1

Double tagging experiments of southern bluefin tuna in the New South Wales (NSW), South Australia (SA), and Western Australia (WA) areas.

Experiment number	Area	Years	Carried out by	Fishing method	Tagging method	Number released	Number[1] recovered	
							with 2 tags	with 1 tag
1	NSW	1963–70	CSIRO	Pole	Board[2]	2770	253	153
2	NSW	1963–70	Fishermen under contract to CSIRO	Troll	Board	9513	3199	862
3	SA	1964–69	CSIRO	Pole	Board	7328	929	300
4	SA	1977	CSIRO	Pole	Board	908	164	54
5	WA	1963–67	CSIRO	Pole	Board	12826	264	264
6	WA	1970–78	WA Dep. Fisheries	Pole	Board	5692	236	120
7	WA	1983	CSIRO	Pole	Cradle[3]	6907	1853	472
8	SA	1984	CSIRO	Pole	Cradle	3211	1117	176

[1]Excludes recoveries for which an accurate recapture date was not available.
[2]Fish placed on a measuring board for tagging.
[3]Fish placed in a specially designed cradle for tagging.

applications, it is necessary that the data be analyzed as a series of separate release sets rather than as a pooled data set, and corresponding shedding-rate estimates are thus required; (2) there are now reliable recovery data for 10,416 double-tagged southern bluefin available for analysis (compared with the 1511 recoveries considered by Kirkwood 1981); and (3) models are now available that utilize exact periods at liberty rather than data aggregated by time period. Provided accurate recapture times are available (as is the case here), these new models are preferable because of their greater ability to deal with low recovery numbers towards the end of an experiment.

Tagging data and tagging methods

The tagging data used in this analysis consist of all records received by 31 March 1987 of southern bluefin that were originally double-tagged and that had accurate recapture dates. Recovery dates were considered accurate if at least the month of recapture was known with certainty. In total, there were 10,416 recoveries that met this criterion. Of these, there were 671 recoveries for which the month of recapture was known but the exact day was uncertain; however in almost all of these cases, the uncertainty was estimated to be no more than ± 5 days.

The data were grouped into eight double-tagging experiments: (1) NSW releases 1963–70 (CSIRO*); (2) NSW releases 1963–70 (fishermen contracted by CSIRO); (3) SA releases 1964–69 (CSIRO); (4) SA releases 1977 (CSIRO); (5) WA releases 1963–67 (CSIRO); (6) WA releases 1970–78 (WA Dep. Fish.); (7) WA 1983 (CSIRO); and (8) SA 1984 (CSIRO). This classification of the data was made to ensure that, within experiments, the geographical area, fish size, tagging and fishing methods, and tagging personnel were as similar as possible.

Except for experiment 2, the primary method used to catch fish for tagging was commercial bait and pole; in experiment 2, trolling was used. In all experiments, fork lengths of the fish selected for tagging were measured before tagging. For the first six experiments, this was done by placing the fish on a measuring board. In experiments 7 and 8, the fish were placed in a specially designed vinyl cradle supported by a metal frame and their fork lengths measured using graduations marked on the cradle. While the fish were restrained on the measuring board or in the cradle, two numbered tuna tags of a standard type (Williams 1982) were inserted forward into the musculature at an angle of about 45°, 1–5 cm below either side of the posterior insertion of the second dorsal fin. Ideally, the tag barb anchored behind the second dorsal fin ray extensions or the neural spines, and in experiments 7 and 8 greater effort was made to achieve this than in earlier experiments.

A summary of the fishing method, tagging method, and the numbers of tuna released and recovered is given for each experiment in Table 1. For ease of presentation, the numbers of recoveries in each experiment are grouped by period at liberty in Table 2; as noted above, exact times at liberty for each recovery were used in the subsequent analyses.

*Tagged by staff of the Commonwealth Scientific and Industrial Research Organization (CSIRO).

Table 2

Numbers of double-tagged southern bluefin tuna, for which accurate recapture dates are known, that were reported to have retained both tags (D) or only one tag (S) on recapture, listed by period at liberty.

Period at liberty (yr)	Experiment number															
	1		2		3		4		5		6		7		8	
	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S
0–1	175	61	2638	467	831	158	128	23	166	84	205	73	1428	314	644	64
1–2	70	61	517	329	51	76	30	15	72	108	23	31	306	102	381	75
2–3	6	21	37	52	15	19	3	11	18	27	2	7	101	40	82	35
3–4	1	1	4	5	11	9	2	4	–	8	3	4	18	16	10	2
4–5	1	1	1	1	10	11	–	–	3	15	1	2				
5–6	–	–	–	1	2	10	–	–	3	9	–	2				
6–7	–	2	1	2	2	7	–	–	1	4	2	1				
7–8	–	2	–	1	2	1	–	–	–	–	–	–				
8–9	–	1	–	1	2	6	1	1	–	4	–	–				
9–10	–	1	–	1	2	–	–	–	–	1	–	–				
10–11	–	–	1	1	–	1	–	–	–	–						
11–12	–	–	–	–	1	1			–	1	–	–				
12–13	–	–	–	–	–	–			–	–	–	–				
13–14	–	–	–	–	–	–			–	2	–	–				
14–15	–	2	–	–	–	–			–	–	–	–				
15–16	–	–	–	–	–	–			–	1	–	–				
16–17	–	–	–	1	–	1			–	–	–	–				
17–18	–	–	–	–	–	–			1	–						

Tag-shedding models

Various models have been proposed to describe the process of tag loss (Beverton and Holt 1957 and reviews by Ricker 1975; Wetherall 1982). Tag losses can be classified as type I losses, which effectively reduce the number of tags released (immediate tag shedding, immediate tagging mortality, and non-reporting), and type II losses which occur steadily over time (natural mortality, fishing mortality, permanent emigration, and long-term tag shedding). Considering the shedding process only, the simplest model is that proposed by Beverton and Holt (1957) for type II shedding, where the instantaneous rate of shedding (L) is constant over time. In this model, if for a fish originally single-tagged, $Q(t)$ is the probability of the tag being retained at time t after release, then

$$Q(t) = e^{-Lt} \quad (1)$$

If immediate tag shedding occurs, with a probability $1-\rho$ of this occurring, then

$$Q(t) = \rho e^{-Lt} \quad (2)$$

In some cases, it may be inappropriate to assume a constant shedding rate. Some tags may deteriorate over time, causing their shedding rate to increase (Baglin et al. 1980). Alternatively, some tags may be come more securely fixed over time, e.g., through the gradual laying down of tissue around the tag, causing the shedding rate to decrease (Kirkwood 1981). More generally, Kirkwood (1981) has noted that if individual tags have a different propensity for shedding, then the apparent average shedding rate will decrease with time at liberty, as the tags with the higher shedding rate are lost first. Kirkwood modeled this process by allowing the shedding rate to be a gamma-distributed random variable, rather than a constant; however, his model did not allow for an increasing shedding rate. An alternative approach was adopted by Wetherall (1982), who assumed that the probability of a tag being shed was time-dependent. He proposed a flexible function that allowed either an increasing or decreasing shedding rate.

In this paper, we adopt a time-dependent shedding-rate model that allows the probability of an individual tag being shed to decrease over time in an identical fashion to the average shedding rate of the Kirkwood (1981) model. In this case, we now assume that the rate of shedding at time t after release follows the functional form

$$L(t) = \frac{b\lambda}{b + \lambda t}.$$

It then follows that

$$Q(t) = e^{\int_0^t L(u)\,du} = \left[\frac{b}{b+\lambda t}\right]^b. \quad (3)$$

Note that as $b \to \infty$, $\left[\frac{b}{b+\lambda t}\right]^b \to e^{-\lambda t}$ and $L \to \lambda$. That is, the variable-rate model reverts to the constant-rate model. If a proportion $1-\rho$ of tags are shed immediately, then

$$Q(t) = \rho\left[\frac{b}{b+\lambda t}\right]^b. \quad (4)$$

Parameter estimation

Because only tag returns with accurate recapture dates are considered, an extension of the maximum likelihood estimation procedure used by Kirkwood and Walker (1984) can be used. Suppose fish are double tagged and all tags not immediately shed have identical shedding probabilities that are independent of their companion tags' status (already shed or still retained). Then, if $p_2(t)$, $p_1(t)$, and $p_0(t)$ are the probabilities of a fish retaining two, one, and zero tags, respectively, at time $t\,(0<t<\infty)$ after release,

$$p_2(t) = Q(t)^2,$$

$$p_1(t) = 2Q(t)\,[1-Q(t)]$$

and

$$p_0(t) = [1-Q(t)]^2.$$

A fish that has shed both tags will not normally be distinguishable from a fish that was never tagged. Consequently, the tag-recapture data consist of recoveries of fish retaining one or more tags. Conditional on retention of at least one tag, the probability of a recaptured fish retaining two tags at time t is

$$\frac{p_2(t)}{1-p_0(t)}$$

and that of a recaptured fish retaining one tag is

$$\frac{p_1(t)}{1-p_0(t)}$$

Following an initial release of double-tagged fish at time $t = 0$, suppose m fish bearing two tags were recaptured at times $t_{2i}(i = 1,\ldots,m)$, and n bearing one tag were recaptured at times $t_{1j}(j = 1,\ldots,n)$. Then, the log-likelihood L of the data, conditional on the recapture times $\{t_{2i}\}$ and $\{t_{1j}\}$, is

$$L = \sum_{i=1}^{m} \ln\left[\frac{p_2(t_{2i})}{1-p_0(t_{2i})}\right] + \sum_{j=1}^{n} \ln\left[\frac{p_1(t_{1j})}{1-p_0(t_{1j})}\right].$$

Estimates of the model parameters incorporated in $p_2(t)$, $p_1(t)$, and $p_0(t)$, and their asymptotic variances, can then be obtained by maximizing L using standard methods (e.g., Bard 1974).

Model selection

For each of the experiments, we attempted to select the most parsimonious model. Accordingly, we first fitted model (4), which incorporates immediate tag shedding and (with $b<\infty$) a time-varying shedding rate. Then likelihood-ratio tests (Kendall and Stuart 1961) were carried out to test the null hypotheses that (1) $\rho = 1$ (no immediate tag shedding), (2) $b = \infty$ (constant shedding rate), and (3) both $\rho = 1$ and $b = \infty$. Unfortunately, since these hypotheses are not fully nested, some ambiguity can still remain. The choice is clear-cut if none of the three hypotheses is rejected, or if all but one are rejected. However, it is possible that while hypothesis (3) is rejected, neither (1) nor (2) is rejected. In that case, there is no reliable basis to distinguish between models (2) and (3).

Particularly when performing non-linear estimations such as these, it is essential to examine the fit of the estimated model to the observed data. Unfortunately, since we are maximizing a likelihood conditional on the observed recapture times, there is no exact way of doing this. As an approximation, however, we can examine the fit of the estimated models to recovery data grouped by time intervals. From the data in Table 2, it is a simple matter (e.g., based on equation 9 in Wetherall 1982) to calculate, for each k, estimates of the proportions of tags shed (P_k) by time t_k, the midpoint of the k-th time interval since release, as well as exact 95% confidence intervals for these proportions based on the binomial distribution. If it is assumed that all tags shed during the k-th time interval were shed at time t_k, then the fitted model and "observed" proportions can be displayed on the same graph. For the grouped data in Table 2, time intervals of one year were used for the first five periods after release. The relatively few longer-term recoveries were grouped into periods at liberty of 5–10 years and 10–20 years.

Table 3

Maximum likelihood estimates of tag-shedding parameters for southern bluefin tuna double-tagging experiments using ungrouped data.

Experiment no.	Selected model	Parameters		
		$\lambda \pm$ SE	$\beta \pm$ SE	$\rho \pm$ SE
1	2	0.29 ± 0.05	∞	0.93 ± 0.02
	3	1.00 ± 0.33	0.26 ± 0.10	1.0
2	2	0.17 ± 0.01	∞	0.976 ± 0.006
3	3	0.78 ± 0.12	0.26 ± 0.05	1.0
4	2	0.17 ± 0.04	∞	0.96 ± 0.01
5	3	1.04 ± 0.28	0.36 ± 0.11	1.0
6	2	0.19 ± 0.05	∞	0.90 ± 0.02
7	3	5.08 ± 2.02	0.031 ± 0.004	1.0
8	2	0.049 ± 0.008	∞	0.970 ± 0.007

Results

Maximum likelihood estimates of the tag-shedding parameters and of their standard errors are given in Table 3. Curves, based on these parameter estimates, that describe the time-dependent probability of tag shedding, together with estimates of the proportion of tags lost (with 95% confidence intervals) based on grouped data, are shown in Figure 1.

In experiment 1, it proved impossible to distinguish either statistically or visually between a constant-rate model with immediate tag shedding (model 2) and a decreasing-rate model with no immediate tag shedding (model 3). Although the plots of $[1 - Q(t)]$ against t (Fig. 1a) are strikingly different for longer recapture times, apparently both can be accommodated by the grouped recovery data because the number of long-term recoveries is small, resulting in wide confidence intervals for proportions shed.

In all other experiments, it was possible to select a single most appropriate model on statistical grounds. However, wide confidence intervals for the estimates of proportions of tags shed were still evident in most experiments for the longer-term recovery periods. In experiment 2 and the medium-term experiments (4 and 6), a constant-rate model with some immediate tag shedding was selected (Fig. 1b,d,f). In the other long-term experiments (3 and 5), model (3) provided the best fit, and the shedding rate showed a marked tendency to decrease with time (Fig. 1c,e).

The most striking difference among the experiments was the very low shedding rates observed in experiments 7 and 8 (Fig. 1g,h) compared with the other experiments. After 4 years, the probability of shedding, as predicted by the fitted models, was approximately 0.2 for experiments 7 and 8, whereas it was 0.5–0.7 for the earlier experiments.

Discussion

The tag-shedding rates estimated for experiments 1–6 are of a similar order to those obtained for southern bluefin tuna by Kirkwood (1981), who used a restricted subset of the data pooled across these experiments. Constant rates of tag shedding have been estimated by Hynd (1969) for southern bluefin tuna (0.26/yr), by Bayliff and Mobrand (1972) for yellowfin tuna (0.278/yr), and by Lenarz et al. (1973) and Baglin et al. (1980) for Atlantic bluefin tuna (0.210/yr and 0.205/yr, respectively). The essentially constant rates estimated in this paper for experiments 2, 4, and 6 are generally slightly lower then these, but still comparable. However, the shedding rates estimated for experiments 7 and 8 are very much lower than for any previously reported tuna double-tagging experiment with substantial numbers of recoveries. The low estimates of shedding rates obtained by Laurs et al. (1976) for north Pacific albacore and Lewis (1981) for south Pacific skipjack were based on very small numbers of tag recoveries.

As mentioned earlier, most previous estimates of tag-shedding rates have been calculated using recovery data grouped by period at liberty. For this method to be effective, the number of observations in each grouping interval must be above a certain minimum. Where the data are sparse, the grouping intervals must cover longer periods. This can result in loss of information, as is seen, for instance, in Table 1 for the longer periods at liberty. Worse, as Kirkwood and Walker (1984) found for a double-tagging data set with very few recoveries, the grouped data estimates may be highly dependent on the grouping intervals used. Here, building on Kirkwood and Walker (1984), we have adopted an estimation procedure that uses exact periods at liberty, which—at least in principle—gets around this problem. However, this is not achieved without a price:

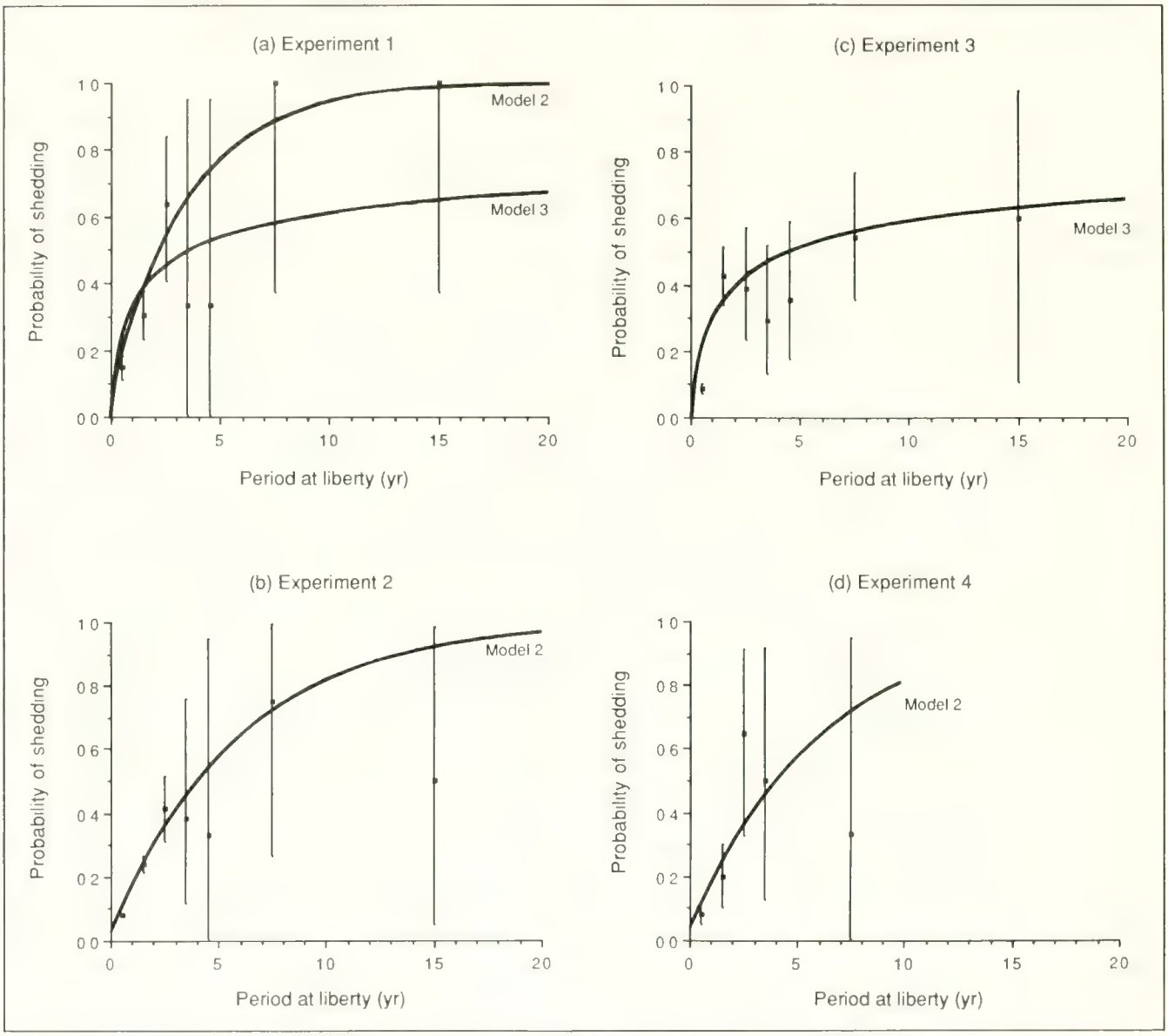

Figure 1

Comparisons of the probabilities of tag shedding by southern bluefin tuna as predicted by the best fitting models, with the proportions of tags shed as calculated from grouped data. Bars represent 95% confidence intervals on the proportions.

having to condition on the observed times at liberty, the calculated standard errors of the estimated parameters are almost certainly biased downwards. As the numbers of recaptures increase and the grouping intervals shorten, estimates based on grouped and ungrouped data should converge. However, the rate of convergence may be slower than might be expected. Table 4 gives parameter estimates that were calculated by applying the Kirkwood (1981) method to the grouped data in Table 2. Comparison of estimates using ungrouped data (Table 3) and grouped data (Table 4) reveals substantial differences, not only in terms of the parameter estimates themselves (e.g., experiments 3 and 5) but even in the model selected (e.g., experiments 6 and 7), despite the relatively large numbers of recaptures.

No formal statistical analysis is needed to conclude that the shedding rates in experiments 7 and 8 are significantly lower that those in experiments 1–6. We believe that the most likely explanation for these reduced shedding rates lies in differences in tags and tagging methods. Some of the tags used in the early experiments were reported to have inadequately attached streamers (Hynd et al. 1967). If so, this would

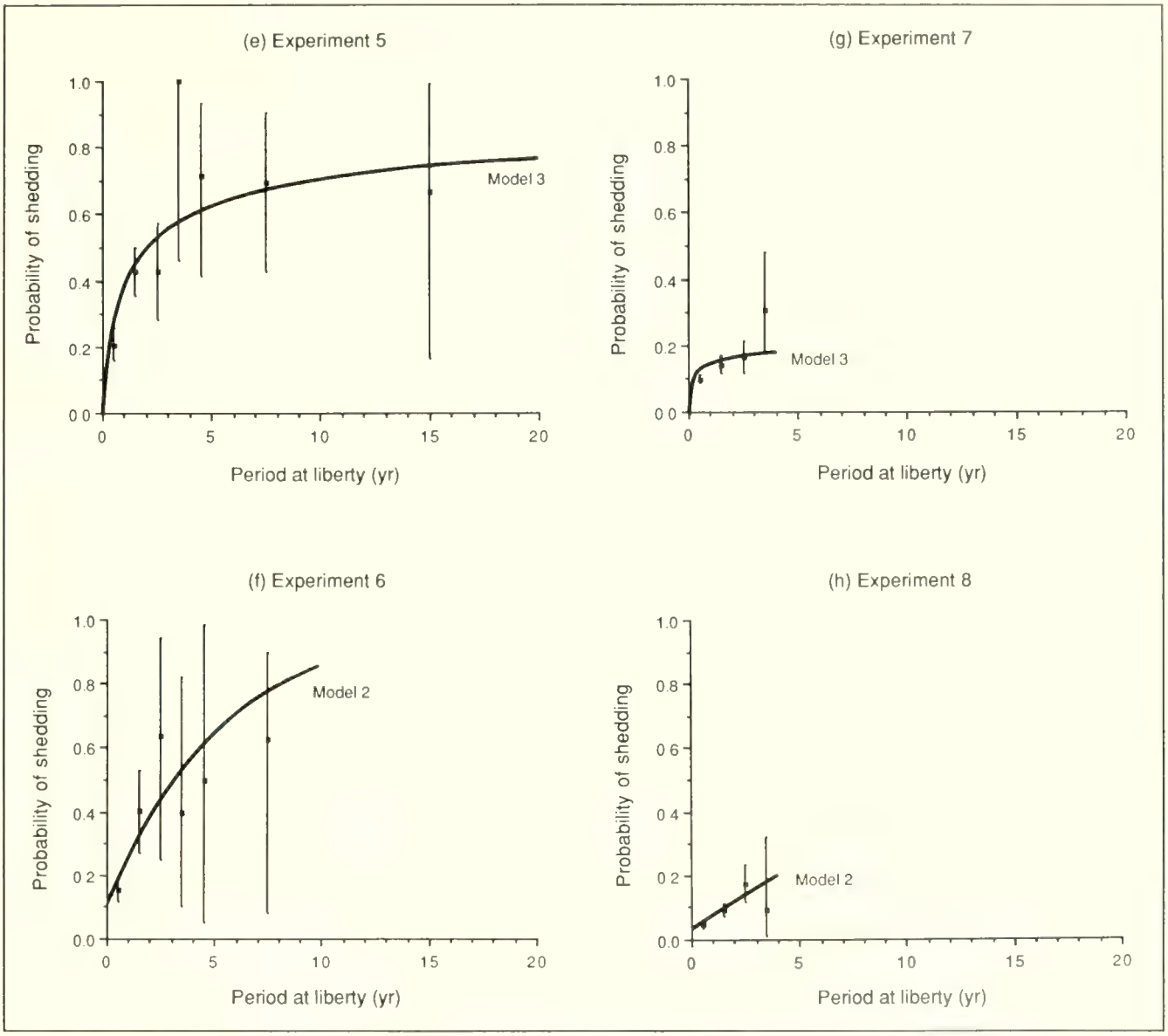

Figure 1 (continued)

Table 4

Maximum likelihood estimates of tag-shedding parameters for southern bluefin tuna double-tagging experiments using grouped data.

Experiment no.	Selected model	Parameters		
		$\lambda \pm$ SE	$\beta \pm$ SE	$\rho \pm$ SE
1	2	0.26 ± 0.05	∞	0.98 ± 0.05
2	1	0.18 ± 0.01	∞	1.0
3	3	0.27 ± 0.07	0.55 ± 0.37	1.0
4	1	0.20 ± 0.04	∞	0.96 ± 0.01
5	3	0.56 ± 0.14	0.66 ± 0.32	1.0
6	3	0.43 ± 0.09	0.53 ± 0.27	1.0
7	2	0.053 ± 0.010	∞	0.93 ± 0.01
8	2	0.055 ± 0.011	∞	0.98 ± 0.01

result in a higher rate of shedding. Tags used in the latest experiments do not appear to have suffered from such defects. In experiments 7 and 8, the use of a specially designed tagging cradle may have resulted in more effective and less traumatic tagging than in earlier experiments, where fish were tagged on a measuring board. Also in experiments 7 and 8, a deliberate effort was made to anchor the tags behind the second dorsal fin ray extensions. Tags successfully attached in this way should have a very small probability of shedding. Unfortunately, little quantitative information is available on the efficacy of the technique of tag attachment adopted for experiments 1–6, but it is known that greater care was taken in tag attachment in the later experiments. If the proportion of ideally attached tags in experiments 1–6 differed markedly from those for experiments 7 and 8, then commensurate differences in shedding-rate estimates would result.

While the lower tag shedding rates in experiments 7 and 8 are obvious on first inspection, the situation is less clear for the earlier experiments. In general terms, the precision of estimates of shedding rates, particularly long-term rates, will increase with the size of the database. On these grounds, pooling of the data for experiments 1–6 would appear to be an attractive option. However, it would be appropriate to do so only if the assumptions underlying the analysis of the pooled data remained valid. Critical among these assumptions is that all tags have identical and independent shedding probabilities. The primary reason for classifying the tag releases in the 1960s and 1970s as six separate experiments was a suspicion that these probabilities may well have been heterogeneous. As mentioned earlier, with this classification we were attempting to minimize within-experiment differences in geographical area, fish size, capture and tagging methods, and tagging personnel. While in principle further subdivision is possible, for example by tagging vessel in order to take account of different tagging teams, we felt this may leave too few data in each subset to obtain reliable estimates of shedding rates. Also, no assertion is made that the classification chosen is an optimal one; indeed it is by no means obvious that suitable criteria for optimality could be defined. A statistical way of examining whether or not it is appropriate to pool data for experiments 1–6 is to carry out a likelihood ratio test of the hypotheses that the tag shedding parameters for each experiment are equal. This hypothesis proved to be resoundingly rejected ($P<0.001$). It appears that pooling is not a viable option for these experiments.

One of the subsequent analyses that we had envisaged for recovery data adjusted for tag shedding involved application of the method of Hearn et al. (1987) to obtain estimates of natural and fishing mortality rates. This method, which is essentially a cohort analysis of the tagging data, gives particular weight to long-term recaptures and therefore requires accurate estimates of long-term shedding rates. Despite the large numbers of recoveries in the experiments described in this paper, precise estimation of long-term shedding rates has not been possible. This is best exemplified in the results of experiment 1, where no single best fitting model was obtained, and for which the point estimates of long-term shedding rates differ markedly. Even where a single best-fitting model was available, considerable uncertainty still remained about the long-term shedding rates. It therefore seems essential to take account of this uncertainty in any subsequent analyses using methods such as that of Hearn et al. (1987). This is the subject of further research.

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Abstract.– Seasonal advection of warm western-boundary current water into the southern Benguela eastern-boundary current region from late spring to early autumn coincides with increased coastal upwelling activity. The combined effect of these two processes is to stabilize the system through intensification of temperature fronts and thermoclines, providing conditions favoring anchovy spawning and larval survival. These conditions appear to be robust to short periods of intense storm mixing and downwelling during summer, and weaken and disappear only with the onset of winter when there is diminished influence of the warm western-boundary current water, downwelling conditions, and increased frequency of storms.

Ocean Stability and Anchovy Spawning in the Southern Benguela Current Region

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The extension of the Hjort (1914) hypothesis by Lasker and his coworkers (Lasker 1975, 1978, 1981a,b) to include the role of a stable ocean in determining fish recruitment has had a profound influence on research into the early life history of marine fish. Lasker's extended hypothesis suggests that ocean stability influences food aggregations for larvae and larval drift and, hence, recruitment strength (Lasker 1981b). In support of Lasker's hypothesis, strong wind events have been found to disrupt anchovy larval food aggregations, and, by inference, to effect larval mortality off California (Lasker 1975) and Peru (Walsh et al. 1980). During such events, larvae can also be entrained within increased offshore Ekman flow and placed outside suitable feeding areas (Walsh et al. 1980, Lasker 1981b). A significant linear relationship between anchovy larval mortality rate and the frequency of calm, low wind-speed periods during the spawning season off California (Peterman and Bradford 1987) provides further evidence of the importance of event-scale disruption of ocean stability.

Parrish et al. (1983) compared the seasonality and geography of sardine and anchovy reproduction in the California, Peru, Canary, and Benguela Current systems with corresponding features of the environment and suggested that patterns of correspondence may indicate the most crucial processes affecting reproductive success. They found that spawning was adapted to avoid times and places characterized by intense turbulent mixing and strong offshore transport.

In this paper we use survey data to provide a finer-scaled description of ocean stability and anchovy spawning than that of Parrish et al. (1983), and suggest that in the southern Benguela Current system anchovy spawning is adapted to seasonal patterns of ocean stability that are resistant to event-scale processes. Local conditions are briefly compared with those in the Southern Californian Bight where Lasker's studies took place, and conclusions are drawn with respect to the influence of ocean stability on survival of the planktonic stages and recruitment in the southern Benguela Current region.

Methods

During the Cape Egg and Larval Programme (CELP), plankton and the environment were sampled at approximately monthly intervals between August 1977 and August 1978 from a grid of stations in the southern Benguela Current region. The purpose of the program was to determine general spawning habitat and time for the major fish species of commercial importance (Shelton 1986). The grid comprised 120 stations posi-

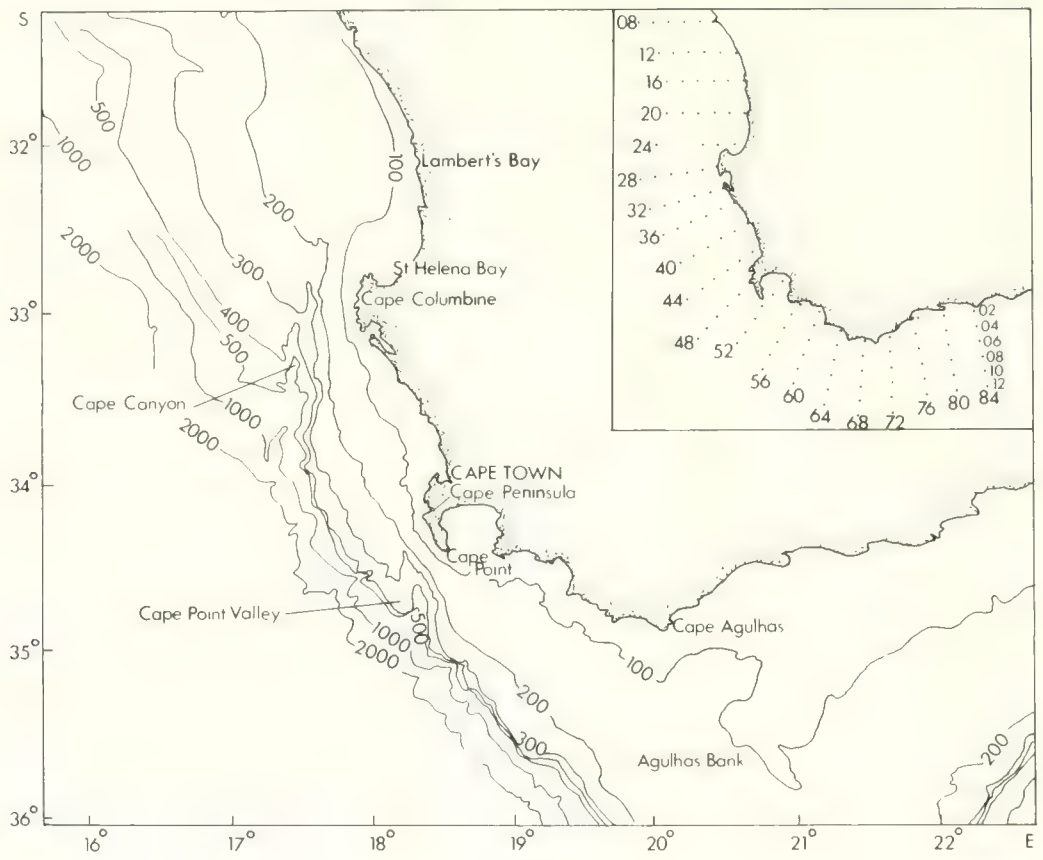


Figure 1

Cape Egg and Larval Programme (CELP) survey grid, southern Benguela Current region, sampled monthly August 1977–August 1978, and general topography of the survey area (depth contours in meters).

tioned at 10-nautical-mile intervals (18.5 km) on 20 transects (Fig. 1).

Vertical profiles of temperature and water samples for measurement of salinity, chlorophyll-*a* concentration, and microplankton density were collected from the water column. Chlorophyll analysis, described in Shannon et al. (1984), was by means the standard photometric method of SCOR/UNESCO Working Group 17 (1966). Microplankton particle concentration was determined by prefiltering 2 liters of the water sample through a 100-μm filter and collecting those particles retained by a 37-μm filter. Particles between 37 and 100 μm correspond to the size fraction considered to be important for first-feeding anchovy larvae (Arthur 1976, Hunter 1977). Particles were counted under a light microscope at 20× magnification and expressed as number per liter. Although all particles were enumerated, only the maximum density at each station of total "esculent" (nutritious to fish larvae [Sharp 1980]) particles are presented, such as copepod eggs, nauplii, copepodite stages, and dinoflagellates. Wind strength and direction were estimated by the lighthouse keeper at Cape Point throughout the period. In order to examine surface drift patterns, 20 plastic drift cards (Duncan 1965) were released monthly at each station sampled.

Fish eggs and larvae were sampled by means of a double oblique haul of a Bongo sampler down to a maximum depth of 100 m. The sampler had a mouth opening of 57 cm and was fitted with 300-μm and 500-μm mesh nets. Counts of anchovy eggs and larvae from the 300-μm unit were standardized to volume or numbers under 10 m^2 using the formula given in Smith and Richardson (1977). In November 1979 and November 1984 the vertical distribution of anchovy eggs and temperature profiles was measured at two localities. Eggs were sampled with Miller nets (Miller 1961) as described in Shelton and Hutchings (1982). Anchovy egg and early-stage larval abundance data from a more extensive grid of stations sampled in November 1983 using a CalVET net (Smith et al. 1985) are also presented.

Results and discussion

Seasonality in temperature and spawning

Both the mean and the coefficient of variation (CV) of sea surface temperature measured over the CELP grid peaked in summer (Fig. 2). This is caused by the seasonal advection of warm water orginating from the western-boundary Agulhas Current into the southern Benguela Current region (Shelton et al. 1985) and the simultaneous increase in coastal upwelling (Andrews and Hutchings 1980). Strong cross-shelf temperature gradients, or fronts, are set up between advected and upwelled water, reflected by the increase in the surface temperature CV. In winter the influence of western-boundary current water is diminished and upwelling is less frequent and less intense (Shelton et al. 1985, Andrews and Hutchings 1980). Consequently, cross-shelf temperature gradients weaken and disappear and mean SST values are lower and have a lower CV, reflecting cool, more isothermal conditions.

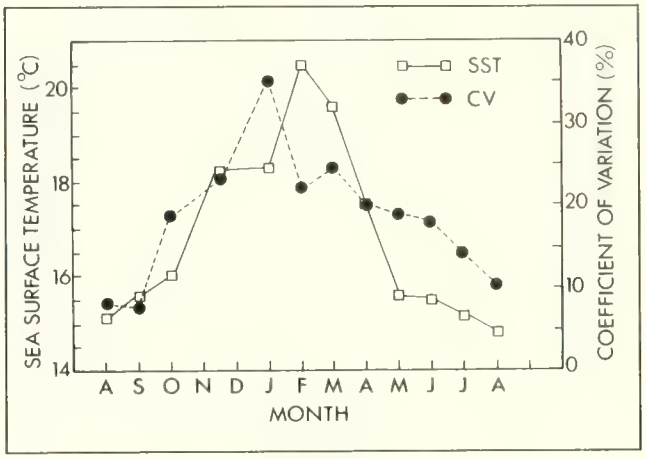


Figure 2
Monthly means and coefficents of variation (CV) of sea-surface temperature (SST) values over the CELP survey grid, southern Benguela Current region, for the period August 1977–August 1978.

Horizontal structure

The changes in temperature structure described above, as well as associated changes in the patterns of abundance of microplankton and chlorophyll-*a*, can be seen in contour diagrams of values for summer and winter (Fig. 3). The strong temperature front that develops along the west coast in summer is clearly visible. Although this front is most persistent between Cape Point and Cape Columbine, and was considered by Bang (1973) to "pivot" at Cape Point, it may extend as far south as Cape Agulhas when upwelling occurs at capes east of Cape Point. At Cape Columbine isotherms tend to diverge offshore, and further north the front is generally weaker and more variable. The density of potential food particles for early-stage larval feeding, as indicated by microplankton and chlorophyll-*a* concentrations, are highest inshore of the temperature front in summer, indicating that the front constrains the offshore Ekman drift of productive upwelled water. In winter when the front disappears, microplankton and chlorophyll-*a* concentrations are generally lower and more dispersed.

Arrows indicating major directions of surface drift over the survey area in summer (January 1978) and winter (August 1977) based on drift-card recoveries are plotted in Figure 4. Of the 24,000 cards released in each month there was a 5% recovery in January 1978 and a 7% recovery in August 1977. There was no clear seasonality in the overall recovery rate. In summer the southern Agulhas Bank area was characterized by onshore surface flow with a westerly component. Some cards released over the western Agulhas Bank moved around Cape Point and up the west coast, and the general pattern of flow inshore of the strong temperature front on the west coast was northwards. North of Cape Columbine there was some evidence of onshore flow. There were very few southern African recoveries offshore of the front, although several cards were recovered along the eastern coast of South America, indicating general offshore flow into the South Atlantic gyre at stations offshore of the front.

In winter, flow in the south was again predominantly onshore, although this time with a marked easterly component east of Cape Agulhas and a westerly component to the west. Several cards released on the western Agulhas Bank were found substantial distances up the west coast, although one card released in the extreme north of the grid travelled against this flow and was recovered on the east coast. Again, few cards were recovered on the coast of southern Africa from releases on the west coast, although there were 10 recoveries from the coast of South America and one recovery from southern California. In comparison with summer, several of these recoveries came from cards released at inshore stations, indicating widespread offshore flow along the west coast in the absence of the front.

Vertical structure

Summer and winter vertical structure of temperature, microplankton density, and chlorophyll-*a* concentration are shown for three representative sections over the survey area in Figures 5–7. A section over the Agulhas Bank (Fig. 5) shows the existence of a strong thermocline in summer between warm water of Agulhas

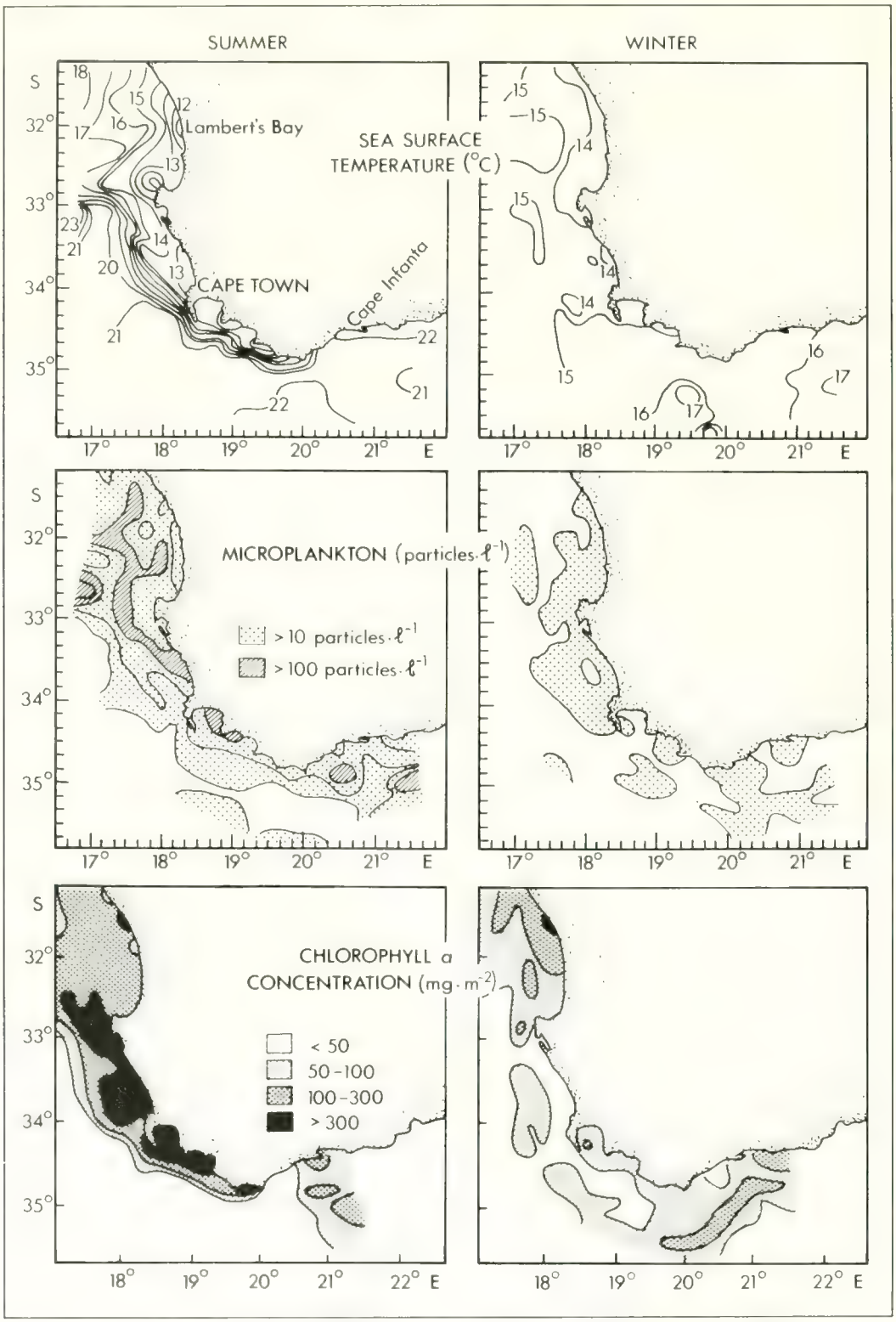


Figure 3

Typical summer (January 1978) and winter (August 1977) patterns of sea-surface temperature, microplankton particle concentrations, and chlorophyll-*a* concentrations over the CELP survey grid, southern Benguela Current region.

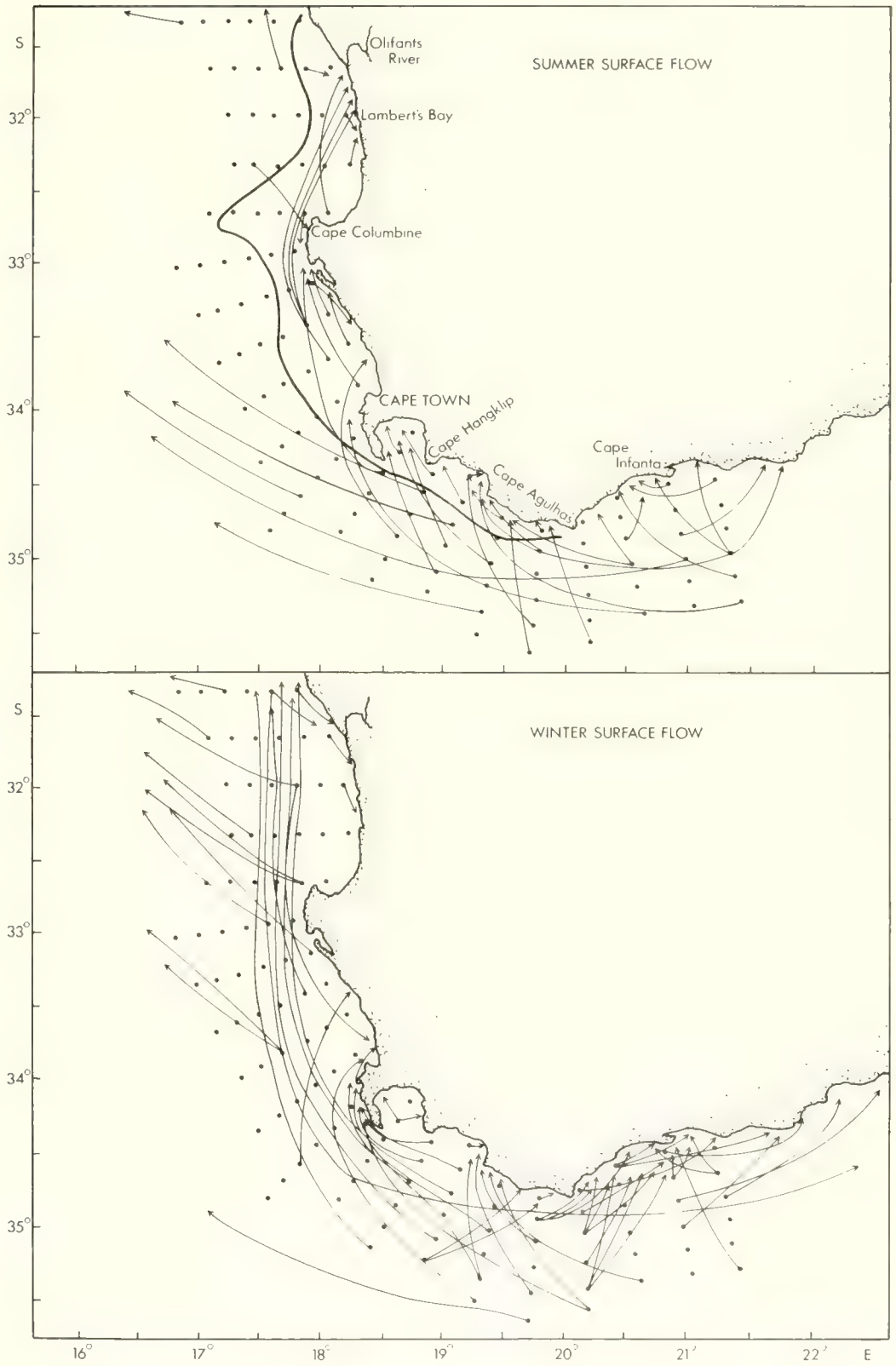


Figure 4

Summer and winter patterns of surface flow in the southern Benguela Current region, gauged from drift-card recoveries from releases of 20 cards at each station in January 1978 and August 1977. Arrows may represent more than one recovery and indicate general direction of flow.

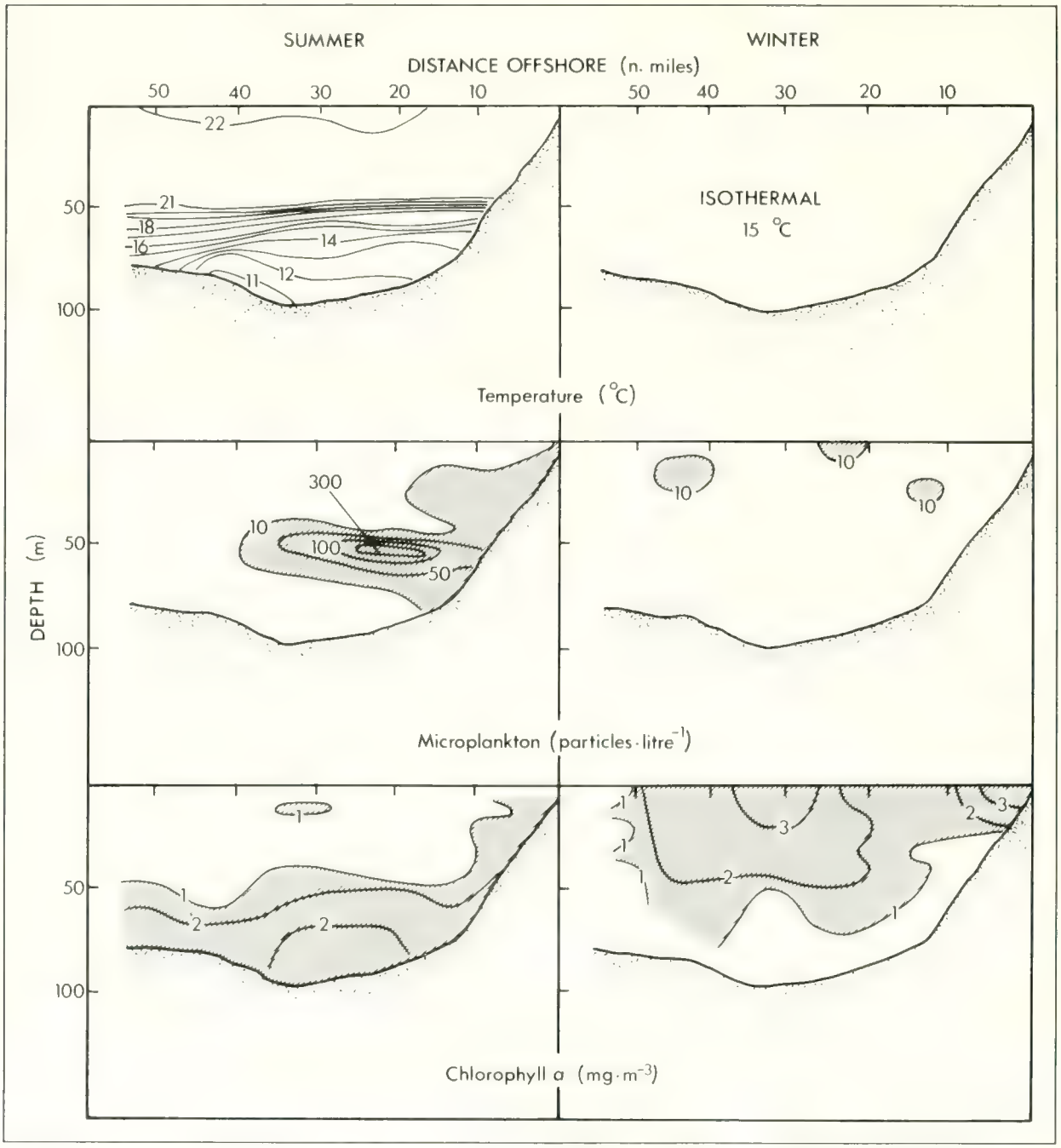


Figure 5

Summer (January 1978) and winter (August 1977) sections of temperature, microplankton, and chlorophyll *a* values along line 76 over the Agulhas Bank, southern Benguela Current region.

Current origin forming an upper mixed layer and cold water that moves onto the Bank along the bottom in summer. The warm layer had very low plankton densities, but enhanced microplankton density and phytoplankton-*a* concentration were associated with the thermocline.

With the onset of winter, the influence of the warm Agulhas Current water over the Agulhas Bank becomes less and heat loss to the atmosphere increases, causing a cooling of the surface layer. Surface cooling combined with the movement off the shelf of the cold bottom layer makes the water column less stable and susceptible to mixing by winter storms (Shannon et al.

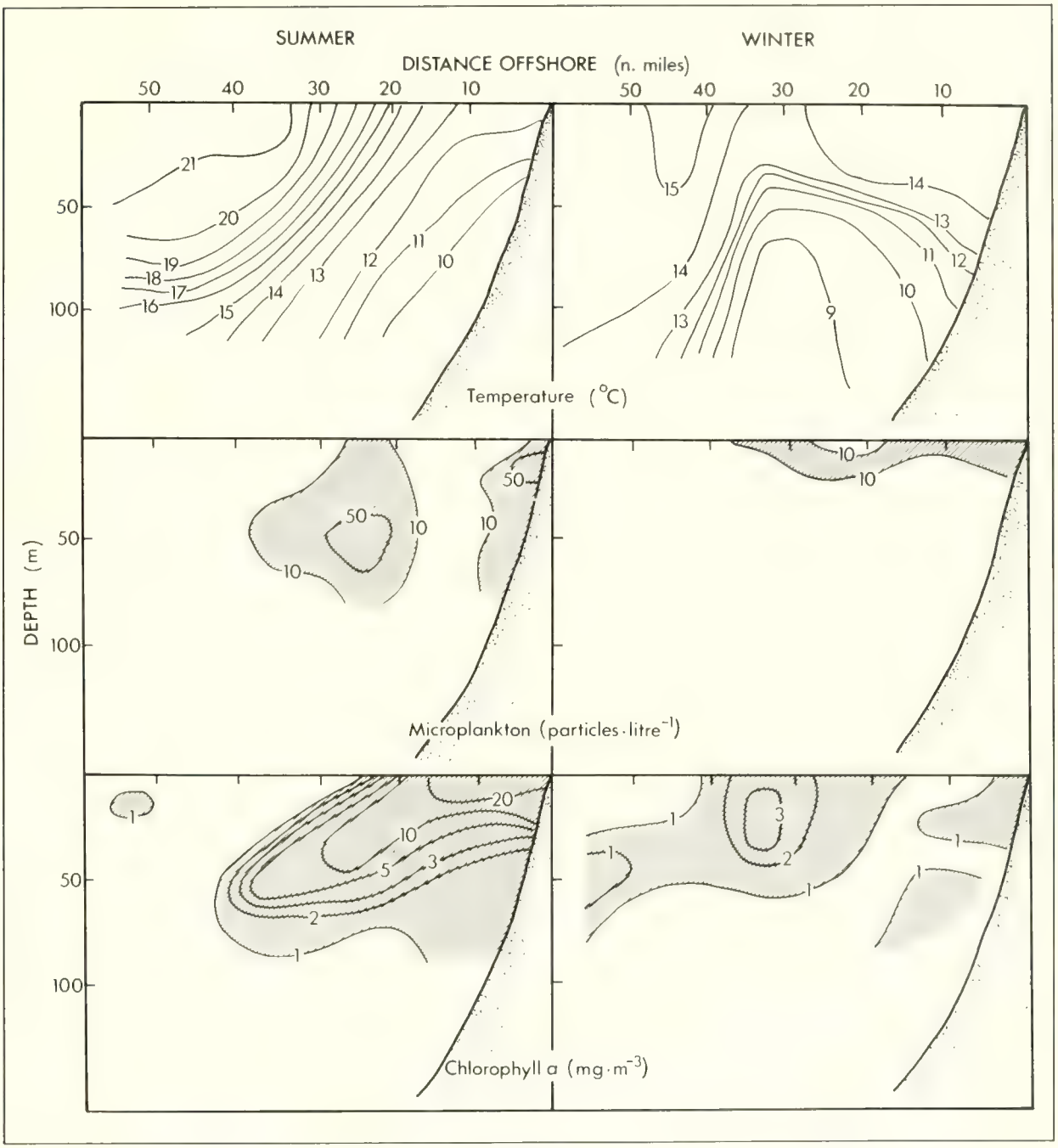


Figure 6

Summer (January 1978) and winter (August 1977) sections of temperature, microplankton, and chlorophyll-*a* values along line 44 just north of Cape Town, South Africa.

1984, Largier and Swart 1987). Microplankton particle concentrations tend to be low in the well-mixed water column but chlorophyll-*a* concentrations can be quite high, either if nutrients accumulated in bottom sediments are mixed into the euphotic zone by strong storm action (Shannon et al. 1984), or if periods of calm weather persist long enough for the water column to stabilize, albeit weakly, and phytoplankton is thereby allowed to remain in the euphotic zone long enough to grow.

A section just north of Cape Town (Fig. 6) shows the strong temperature front in summer between cold upwelled water inshore and warm water offshore. Enhanced levels of microplankton occurred in the vicinity

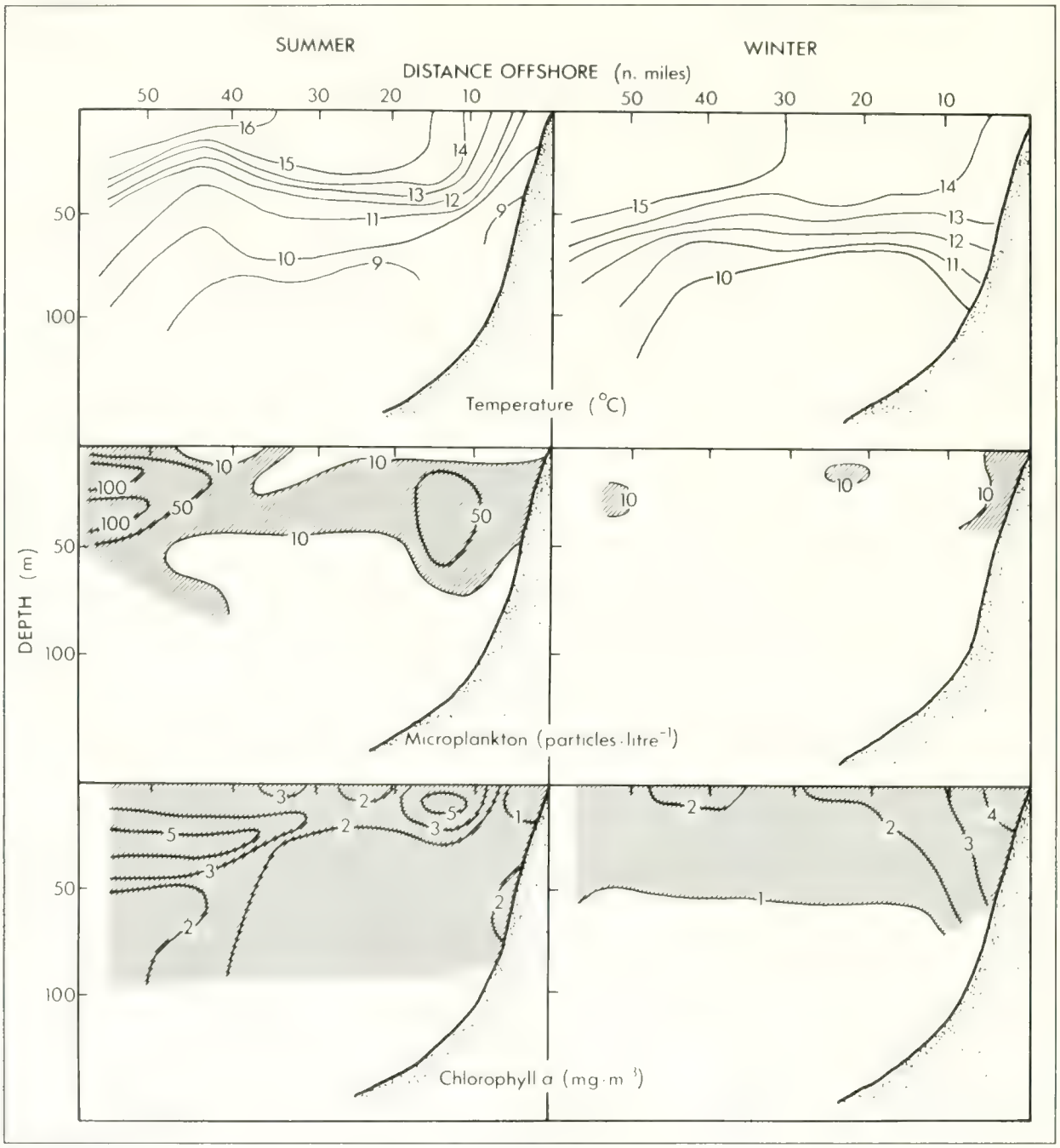


Figure 7

Summer (January 1978) and winter (August 1977) sections of temperature, microplankton, and chlorophyll-*a* values along line 16 in the vicinity of Lambert's Bay, South Africa.

of the front as well as close inshore, and high levels of chlorophyll-*a* were found inshore near the surface, declining in concentration and following the isotherms into deeper water in the vicinity of the front. Offshore of the front, both chlorophyll-*a* and microplankton levels were negligible. A similar pattern was noted in a transect of the front off Cape Columbine in December 1984, with copepod nauplii and copepodites concentrated in the front and chlorophyll-*a* values increasing towards the coast, inshore of the front (Armstrong et al. 1987). Although the front may persist as a subsurface feature in winter, even during prevalent downwelling conditions, it is much weaker as a consequence of cooler water offshore. Microplankton and chlorophyll-*a*

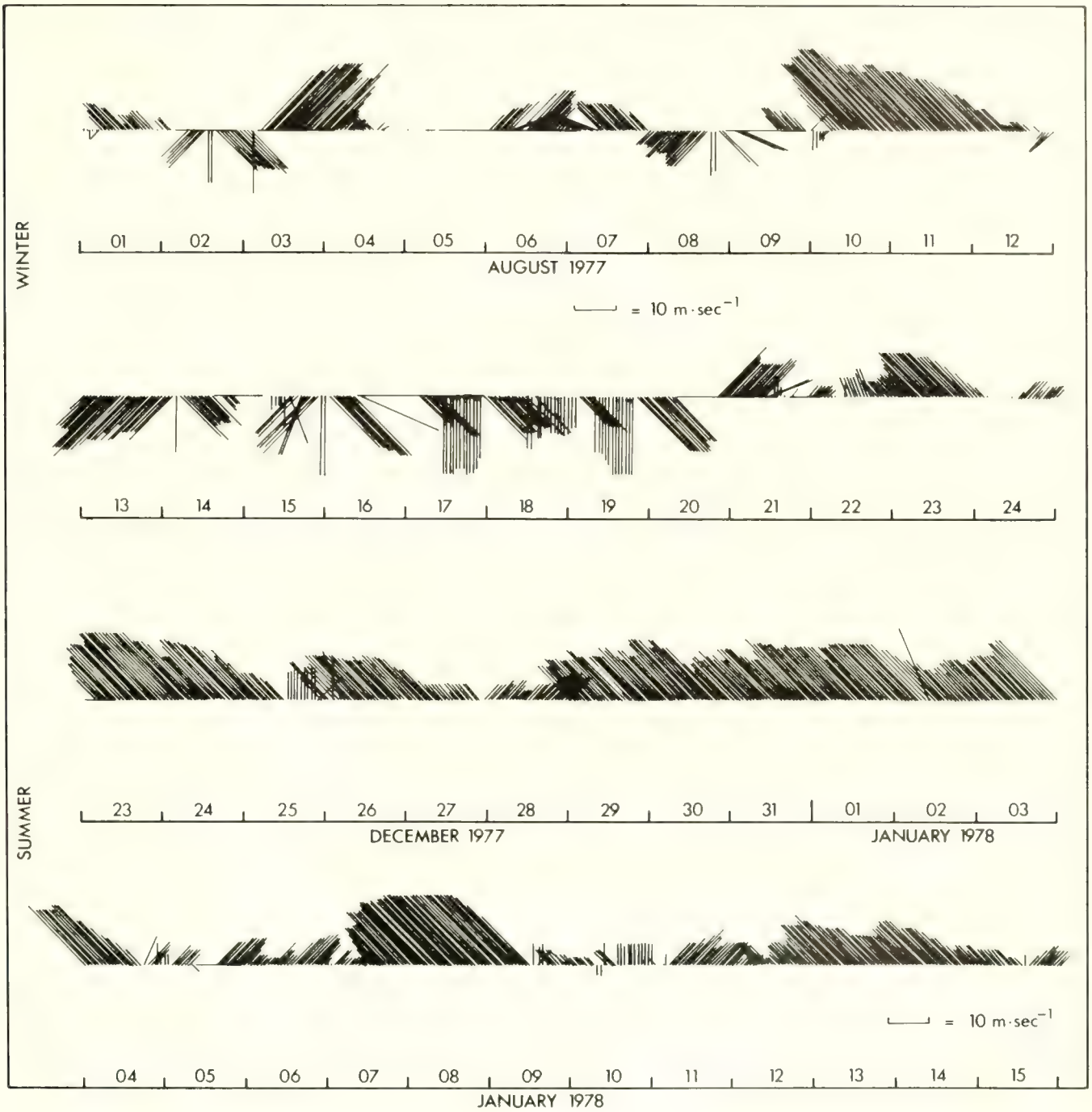


Figure 8

Wind stick diagram for the period 23 December 1977–15 January 1978 and 1–24 August 1977, showing tyical summer and winter patterns of wind stress measured at the lighthouse at Cape Point, South Africa.

values are generally much lower and more dispersed over the west coast between Cape Point and Cape Columbine in the absence of the surface front in winter.

A section on the west coast off Lambert's Bay (Fig. 7) shows a moderately strong thermocline with coastal upwelling in summer. Moderate-to-high levels of microplankton and chlorophyll-*a* extending to the limit of the grid in the top 50 m are typical of the area at this time. In winter the thermal structure is similar, but with less upwelling activity and cooler water offshore. Although microplankton levels were low in the section shown, widespread moderate levels of chlorophyll-*a* are quite

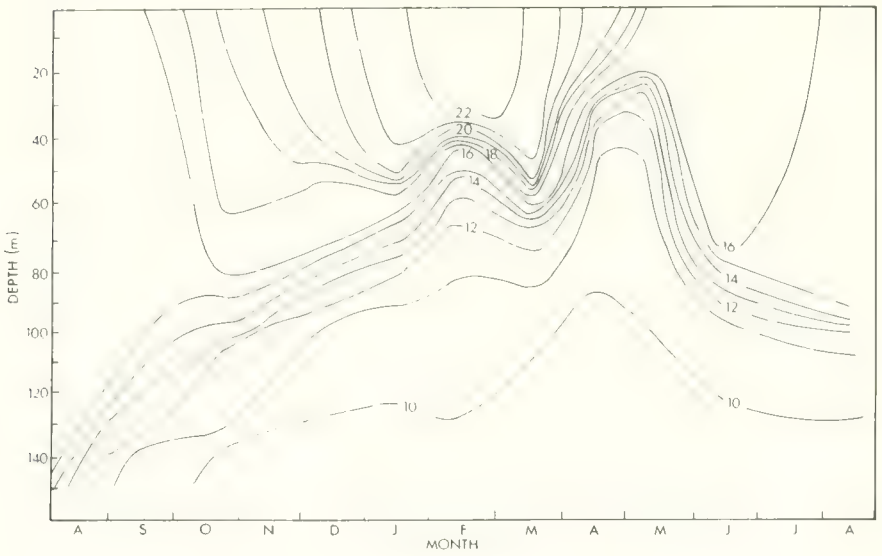


Figure 9
Variability in the vertical temperature structure at station 64-06 on the Agulhas Bank, southern Benguela Current region.

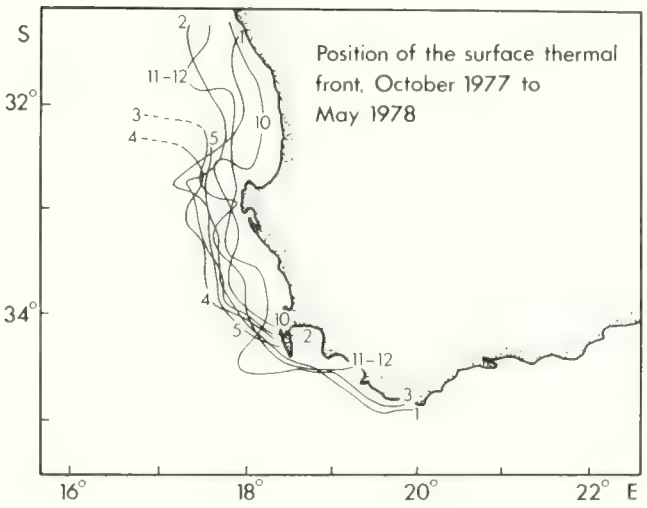


Figure 10
Variability in the position of the surface temperature front in the southern Benguela Current region, spring 1977 through autumn 1978. (Numbers refer to months of the year, e.g., 10 = October 1977, 2 = February 1978.)

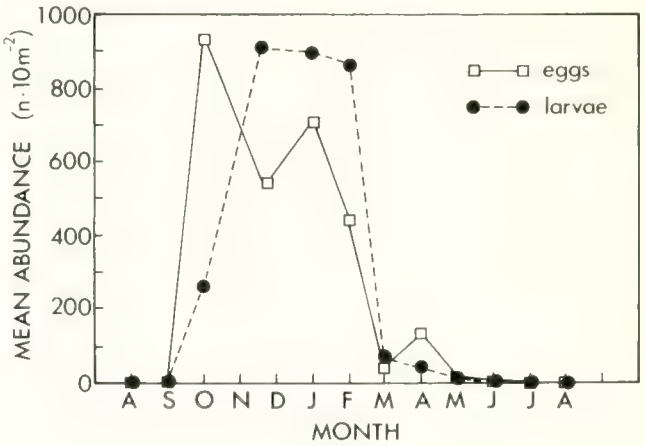


Figure 11
Monthly mean abundance of anchovy eggs and larvae over the CELP survey grid, southern Benguela region, for the period August 1977–August 1978.

typical for the recruitment area in winter, as shown in Figure 3.

Robustness to event-scale processes

Wind stick diagrams of wind strength and direction estimated by the lighthouse keeper at Cape Point (Fig. 8) show that winter is characterized by frequent periods of strong northerly wind interspersed with southerly winds and calm, whereas in summer strong upwelling-favorable southeasterlies dominate, alternating with brief periods of calm and occasional wind reversals. Despite event-scale forcing of this nature, contoured monthly temperature profiles through the water column over the Agulhas Bank show strong stratification persisting over several months of the spring-to-autumn period, weakening and disappearing with the onset of winter (Fig. 9). Similarly, although erratic in appearance and position to the north and south, the temperature front in the transport area between Cape Point and Cape Columbine persists as a stable feature for up to 8 months of the year (Fig. 10), despite event-scale variability in the wind field. During lulls in upwelling the front may weaken at the surface and move inshore, at which time the temperature discontinuity may be most apparent in the form of a thermocline, but it persists as a subsurface feature further offshore (Shelton

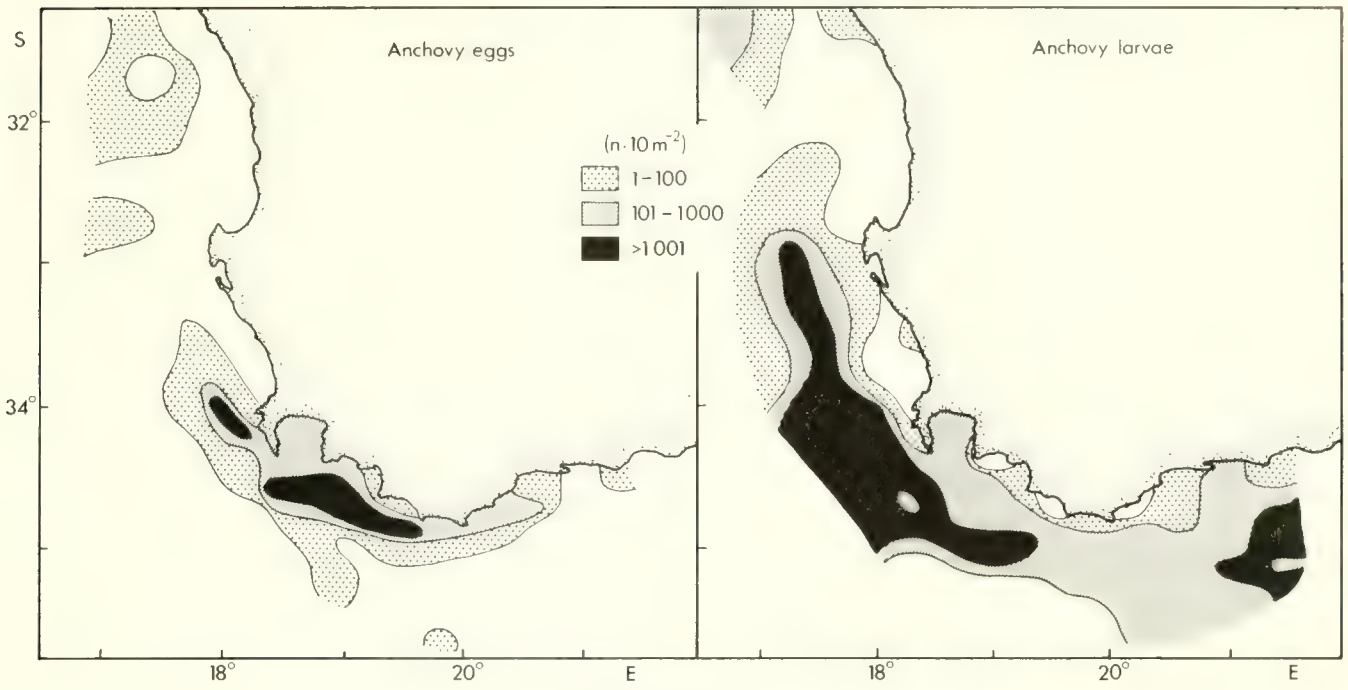


Figure 12

Anchovy egg and larval abundance patterns over the CELP survey grid, southern Benguela Current region, in January 1978, a month of peak spawning.

1986). With the next pulse of upwelling, the isotherms flip to a more vertical orientation and the front moves offshore again, to an average position over the inner shelf break (200-m contour).

Anchovy spawning, transport, and recruitment in relation to ocean stability

Anchovy eggs are generally absent or in very low abundance in the plankton in autumn and winter when the region is cool and isothermal (March–August, Fig. 11). With the onset of spring (September–November) both egg and larval abundance increases rapidly, reaching a peak in late spring or early summer when both the mean temperature and the CV are high, and then decreasing to low numbers over the autumn.

Anchovy spawning is typically most intense south and east of Cape Point over the broad Agulhas Bank (Fig. 12). The vertical distribution of anchovy eggs in the spawning area on the Agulhas Bank (Fig. 13a) is restricted almost entirely to the warm upper mixed layer, above the strong thermocline that forms in summer at about 50 m. On the west coast a transect bisecting the front in the vicinity of the Cape Peninsula shows that anchovy eggs extending up the west coast are concentrated within the frontal zone (Fig. 13b). Anchovy larvae (Fig. 12) are generally more widespread over the Agulhas Bank than the eggs as a result of dispersal, and in particular extend further up the west coast, often as far as Cape Columbine, in the vicinity of the front. Recent samples from a more extensive grid of stations confirm these patterns (Fig. 14).

Based on these patterns of anchovy eggs and larval abundance and the catch pattern of recruits in the commercial fishery (Crawford et al. 1980 and Crawford 1980), the habitat of the anchovy in the southern Benguela region can be divided into spawning, transport, and recruitment areas (Fig. 15). The role of ocean stability in each of these three areas can be evaluated.

Anchovy spawning is highly seasonal, peaking in summer when the southern Benguela region is most structured by temperature fronts and thermoclines under the simultaneous influence of advected warm western-boundary current water and coastal upwelling. The spawning area is characterized by a strongly stratified, stable water column throughout summer. Stratification is resistant to event-scale mixing processes and only weakens with the reduced influence of eastern-boundary current water on the Bank and the retraction of the cold bottom layer with the onset of winter. Winter storms are then able to mix the entire water column creating isothermal conditions which persist until the onset of summer. The warm, uniform surface layer over the Agulhas Bank in summer provides conditions conducive to rapid anchovy egg development; below 14°C anchovy egg development in the

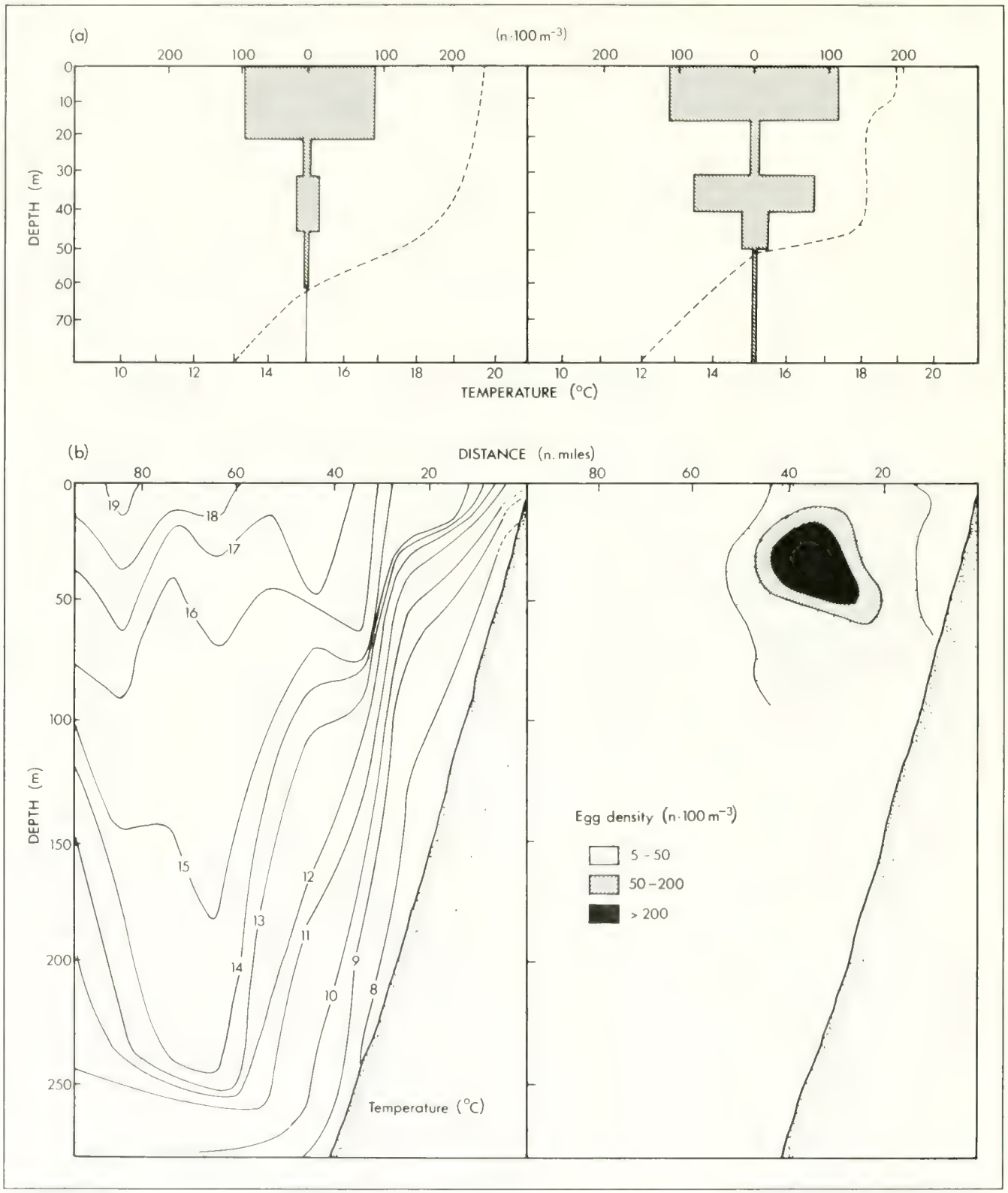
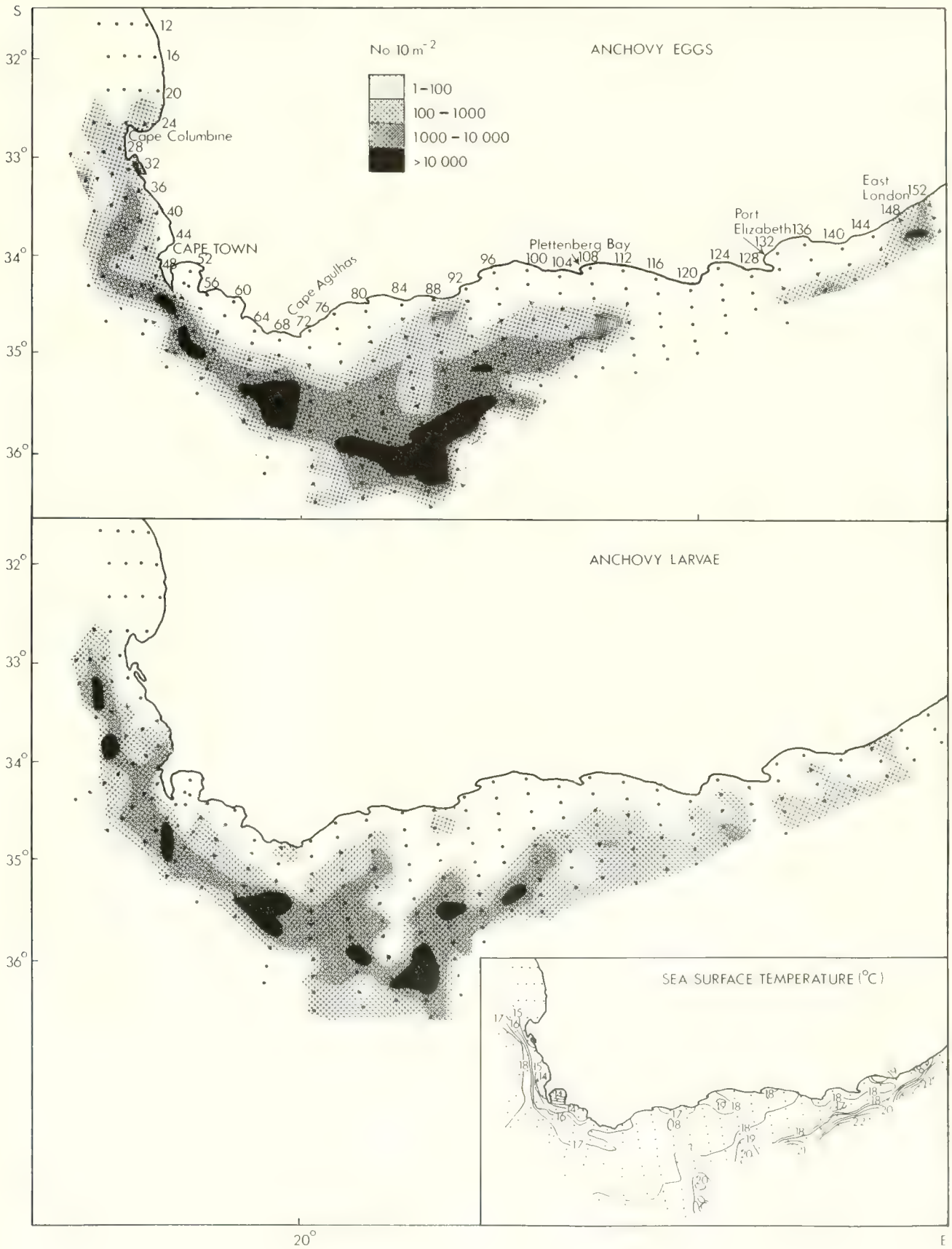


Figure 13

(a) Vertical distribution of eggs and temperature at depth for two stations in the anchovy spawning area, southern Benguela Current region, November 1984. (b) Vertical sections of temperature and anchovy egg abundance measured along a transect bisecting the temperature front off the Cape Peninsula, South Africa, November 1979.

Figure 14

Pattern of abundance of anchovy eggs and larvae in November 1983 from an extensive survey grid covering nearly the entire anchovy spawning area in the southern Benguela Current region.


ANCHOVY EGGS
No 10 m⁻²
1–100
100 – 1000
1000 – 10 000
> 10 000
Cape Columbine
CAPE TOWN
Cape Agulhas
Plettenberg Bay
Port Elizabeth
East London
ANCHOVY LARVAE
SEA SURFACE TEMPERATURE (°C)
S
32°
33°
34°
35°
36°
20°
E

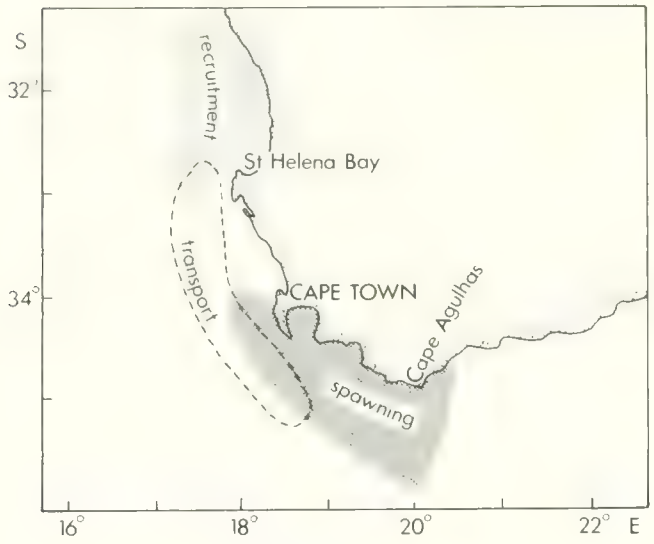


Figure 15
A generalized representation of anchovy spawning, transport, and recruitment areas in the southern Benguela Current region.

laboratory is very slow and hatching larvae are deformed (King et al. 1978). Below the warm surface layer a strong thermocline at about 50 m is associated with subsurface maxima of microplankton and chlorophyll-*a*, facilitating the survival of early-stage larvae that require high concentrations of food particles within a suitable size range (Lasker et. al. 1970).

Spawning conditions in the southern Benguela appear to be in marked contrast with conditions in the spawning ground of the Northern anchovy *Engraulis mordax* in the Southern California Bight where Lasker's studies were carried out. Surface temperatures in the Southern California Bight given in Lasker (1981b) are some 3–5°C lower than over the Agulhas Bank during the respective spawning seasons. Vertical temperature structure during the spawning season off southern California, as shown in Lasker (1978), is quite variable, with generally weak stratification susceptible to mixing. The chlorophyll-*a* layer disrupted by storm mixing in April 1984 was at about 15 m (Lasker 1975), in contrast to the deeper maxima on the Agulhas Bank. Although maximum chlorophyll-*a* values before storm mixing in the layer off California in April 1974 are similar to those recorded in the Agulhas Bank layer, microplankton particle concentrations over the Agulhas Bank do not reach the high values recorded by Lasker (1981b) because dinoflagellates are not as common as in the Southern California Bight, possibly due to persistent strong winds (Parrish et al. 1983), which thoroughly mix the relatively deep, upper mixed layer.

From the the spawning area in the south, the drift of eggs and early-stage larvae is primarily northwestwards, into the west coast transport area. Bang (1973) and Bang and Andrews (1974) have documented the presence of a strong northward-flowing jet current associated with the front which is a prominent feature of this area in summer. The role of this jet in transporting anchovy eggs and early-stage larvae from the Agulhas Bank spawning ground to the west coast nursery area has been examined and described in Shelton and Hutchings (1982). Drift-card recoveries for summer support their interpretation. In the transport area, enhanced levels of chlorophyll-*a* and microplankton associated with the inshore and frontal zone may be important in early-larval survival. Despite predominantly southeast winds in summer, facilitating offshore Ekman flow and upwelling at the coast, the offshore loss of eggs and larvae along the west coast may be small because of the constraining influence of the front. However, there is frequently an offshore divergence of the front off Cape Columbine, following the orientation of bottom contours, and this may be associated with the "leaking" of water containing larvae from the productive coastal region (Shelton et al. 1985, Shelton 1986).

Onshore flow north of Cape Columbine facilitates penetration of the productive recruitment area by larvae. Positioned downstream of the major sites of upwelling at Cape Columbine and Cape Point, the frontal structure dominating the transport area in summer gives way to more gently sloping isotherms north of Cape Columbine where the shelf widens. Because of lower average wind speeds (Hutchings et al. 1988), upwelling is milder than in the transport area and a vertically stable water column is a persistent feature. Enhanced levels of microplankton and chlorophyll-*a* characterize the inner shelf in this area throughout the year (Hutchings 1981), providing suitable conditions for the survival and growth of anchovy recruits.

The patterns of ocean stability described above, based largely on survey data, appear to have played a major role in shaping the spawning behavior observed by anchovy in the southern Benguela region. Upwelling generates the high levels of plankton production that support the spawning biomass of up to 2 million tons of anchovy estimated for the area (Armstrong et al. 1988), but the associated processes of turbulence and offshore Ekman flow present special problems to the plankton stages that have to be solved through evolutionary adaptation. In the southern Benguela region this appears to have been brought about by the selection of times and areas of spawning which make best use of seasonal and spatial patterns of ocean stability to provide suitable food concentrations and favorable transport.

Survey data for the southern Benguela therefore tends to confirm the conclusions from the larger-scale

comparative study of eastern-boundary currents by Parrish et al. (1983) that the spawning habits of anchovy (and sardine) attempt to minimize both wind-induced turbulent mixing and offshore-directed transport. Bakun (1985) argues that the results of Parrish et al. (1983) strengthen the relevance of Lasker's hypothesis to modeling recruitment and exploratory data analysis. However, if anchovy populations in the different eastern-boundary current regions have essentially "solved" the problems of disruptive turbulence and unfavorable transport, "mistakes" should be rare and difficult to find in the field. The fact that event-scale disruptive turbulence has been observed in the spawning area off southern California and that the incidence of calm periods can be statistically related to daily larval mortality rate (Lasker 1975, 1981b; Peterman and Bradford 1987) suggests that such "mistakes" do occur despite adaptations. Even so, they may be undetectable in recruitment measurements, either because of large and often unquantified measurement error, or because the "mistakes" are masked by a well-developed suite of "bet-hedging" traits (Shelton 1987). Estimates of anchovy recruitment (with error bars) for the southern Benguela population based on direct surveys (Butterworth 1989, Fig. 16) show less variability than anticipated in the literature (e.g., Beddington and Cooke 1983), although the time series is still too short to be conclusive.

If the southern Benguela anchovy population is adapted to local persistent patterns of ocean stability and is well-buffered against event-scale variations through bet-hedging, a prerequisite for detectably poor recruitment at moderate spawning stock sizes may be season-long weakening or disruption of the stability patterns in either the spawning, transport, or recruitment areas. Such conditions would probably arise if the influence of Agulhas Current water over the Agulhas Bank and on the west coast were reduced, particularly over the summer period.

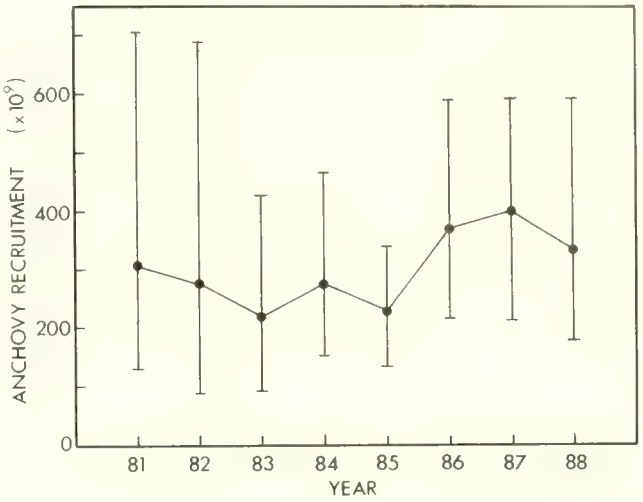


Figure 16

Estimates (median and 95% confidence interval) of annual anchovy recruitment for the southern Benguela population, deduced from direct survey results to July 1988 (Butterworth 1989).

Acknowledgments

We acknowledge the input of several of our colleagues at the Sea Fisheries Research Institute, Cape Town, to the Cape Egg and Larval Programme. In particular, Garth Newman and Vere Shannon provided much of the impetus for the initiation of CELP, and Alan Robertson, Hennie Crous, Frans Kriel, Deon Horstman, Donald Alexander, Robert Cooper, Gustav Wehmeyer, Jan Van der Westhuizen, Chris Jeenes, John Giddey, and Christine Illert gave excellent technical support during its execution. Colleagues at the NMFS Southwest Fisheries Center, La Jolla, particularly the group formally headed by Reuben Lasker, are thanked for their advice and encouragement with respect to the studies of anchovy early-life history in the Benguela Current system. We dedicate this paper to the memory of Reuben.

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Abstract.—A total 3236 km of boat and aircraft surveys was conducted in the northern Gulf of California in search of the vaquita *Phocoena sinus* in 1986–1988. Vaquita were seen on 51 occasions, representing an estimated 96 individuals. Forty-three porpoises (19 sightings) occurred during 1715 km of vessel transects, a rate of 2.51 individuals/100 km of surveys. The number of sightings relative to the extent of the survey emphasized the rarity of the porpoise and is a cause for concern regarding the vulnerability of the population. All sightings of vaquita occurred north of lat. 30°45′N, and all but two sightings (96.1%) occurred less than 40 km from San Felipe, Baja California Norte. Porpoises were observed in small groups (≤3 individuals) in all but five sightings. The mean group size was 1.9 ± 1.24 SD individuals, and the mode was 1. All sightings occurred in water depths of 13.5–37.0 m ($\bar{x}$ 26.1 ± 6.18 SD), with water clarity at these localities ranging from 0.9 to 12 m. Calves represented 9.37% of all individuals sighted. Unconfirmed sightings suggest that the porpoise is present in the southern Gulf of California. Fishermen interviewed in San Felipe, Baja California Norte, were familiar with vaquita, and some have caught the porpoise in gillnets.

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Occurrence and Distribution of the Vaquita *Phocoena sinus* in the Northern Gulf of California

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The vaquita *Phocoena sinus* (Norris and McFarland 1958) is among the rarest and least understood of the Cetacea. In the 30 years following its initial description (Norris and McFarland 1958) very little new information about the porpoise had been obtained. Brownell (1986) reported that only 45 confirmed records of vaquita existed. These consisted of skulls and skeletons (Noble and Fraser 1971, Orr 1969) and about 20 reported sightings obtained between 1958 and 1986 (Norris and McFarland 1958, Norris and Prescott 1961, Villa-R. 1976, Wells et al. 1981). However, Brownell (1986) argued that only four of the sightings were valid.

Increased study of the porpoise in recent years has yielded new information through descriptions of recovered specimens (Magatagan et al. 1984, Brownell et al. 1987), reported sightings (Robles et al. 1986, Vidal et al. 1987, Silber 1988), and behavioral accounts (Silber et al. 1988). Norris and McFarland (1958) described the range of *P. sinus* as occurring in the upper Gulf of California and probably extending south along the Mexican coast, but Brownell (1986) maintained that the range was limited to the upper Gulf of California.

The vaquita population has been impacted by gillnetting activities and other forms of habitat degradation in recent decades (Brownell 1983, Barlow 1986). The species continues to experience mortality at an unknown rate in gillnets (Brownell 1983, Silber 1988) set primarily for totoaba *Totoaba macdonaldi* and various species of shark.

The objective for the initial year of the present study (1986) was to locate *P. sinus*, and subsequently (1987, 1988) to gather information on the ecology and distribution of the porpoise. Visual surveys were conducted from boat and aircraft in an attempt to determine the vaquita's distribution, range, and habitat utilization. Reported here are the results of three seasons of study on the vaquita conducted in the northern Gulf of California in the springs of 1986–88. I have also included a discussion of unconfirmed sightings in the southern Gulf that may reflect the historical range of *P. sinus*.

Materials and methods

Vessel surveys and sighting data

Boat surveys for *Phocoena sinus* were conducted in the northern Gulf of California using an 8-m Boston Whaler. A total of 1715 km of survey transects was conducted on 71 days during the three years (Figs. 1, 2a). The study was conducted in the spring months because (1) operational costs and logistic (e.g., boat time) restrictions limited field work duration, (2) conversations with fishermen in the upper Gulf in 1986 suggested that vaquita were most abundant (perhaps only present) in March–May, and (3) the number of sightings that we obtained (two porpoises in 485 km sur-

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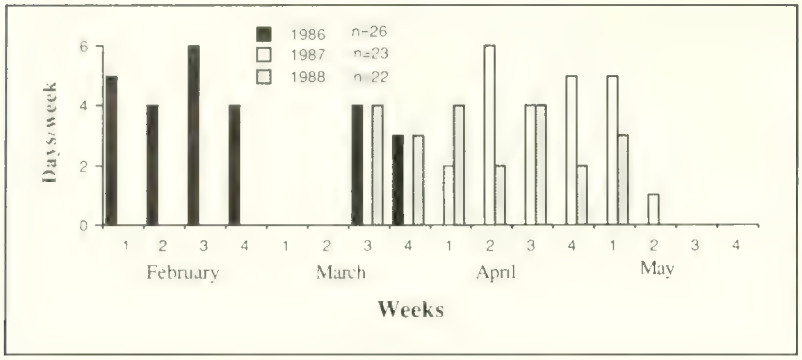

Figure 1
Number of days per week spent conducting transects and observations of *Phocoena sinus* in 1986, 1987, and 1988.

veyed) in February 1986 appeared to support information gathered from fishermen. For these reasons, the decision was made to concentrate survey efforts in March–May, when the likelihood of encountering the porpoise was believed greatest.

During vessel transects, two to four observers positioned 3.5 m above the water surface searched with unaided eyes and binoculars (7 and 10×) the area in front, and about 200–300 m on either side, of the vessel's track. Observers also regularly scanned to greater distances. During all surveys the vessel traveled consistently 10–11 km/hour. Transects conducted in 1986 were restricted primarily to nearshore areas. In subsequent field work inshore surveys were augmented by transects farther from shore.

For each porpoise sighting, the number of individuals seen was estimated and sighting locations were determined by triangulation from landmarks. Water depths were obtained with a JRC color video depth sounder or from a nautical chart. Water clarity (using a Secchi disc) and temperature were measured at most sighting locations. Sea states were obtained by visual estimate according to the Beaufort scale. No surveys were conducted when sea state exceeded Beaufort 3, and the majority were conducted in sea states of 1.

Aerial surveys

Limitations imposed by time, weather, and financial constraints prevented repeated vessel surveys south of lat. 30°30′. However, aircraft surveys were conducted as far south as lat. 29°34′N (Fig. 2b). A total of 1521 km was flown on three days, 3–5 May 1988, concentrating on the upper Gulf.

Fishermen interviews

Fishermen in San Felipe, Baja California Norte, and in the vicinity of La Paz, Baja California Sur, were interviewed in an attempt to obtain qualitative information with regard to the natural history, range, and distribution of the vaquita. Questions were asked regarding type of fishing, target species, years of employment, and location of fishing. The men were asked if they recognized vaquita after viewing photographs of living and dead *P. sinus* and other odontocetes common to the area. The interviews were intended as general informational surveys of local knowledge to direct future study of vaquita and preliminary assessments of fishing effort and vaquita entanglement rates. Information derived from interviews with fishermen has been presented, although questioning methodology and sample sizes were insufficiently rigorous to draw definitive conclusions with regard to vaquita distribution.

Results

Vaquita sightings

Vaquita were seen on 51 occasions, representing an estimated 96 individuals during boat and aircraft surveys (Table 1). A total of 43 porpoises was seen while conducting vessel transects, a sighting rate of 2.51 individuals/100 km surveyed. The remainder of the sightings occurred while tracking porpoises, collecting other types of data, or otherwise not engaged in visual transects. The paucity of sightings relative to the extent of the survey emphasized the rarity of the porpoise.

All sightings of vaquita occurred north of lat. 30°45′N, and all but two sightings (96.1%) occurred less than 40 km from San Felipe, Baja California Norte (Fig. 2a). Most sightings (94.2%) occurred in sea states 0 or 1 (Fig. 3). In 90.2% ($n = 46$) of all sightings, porpoises were observed in small groups (≤3 individuals). Mean group size was 1.9 ± 1.24 SD individuals per group (Table 1) and the group size mode was one (Fig. 4). For 86.3% ($n = 44$) of all porpoise sighting locations, water depths ranged from 21 to 35 m ($\bar{x}$ 25.7 ± 6.36 SD; overall range 13.5–37.0) (Fig. 5), and most sightings occurred 11 to 25 km from the nearest shore

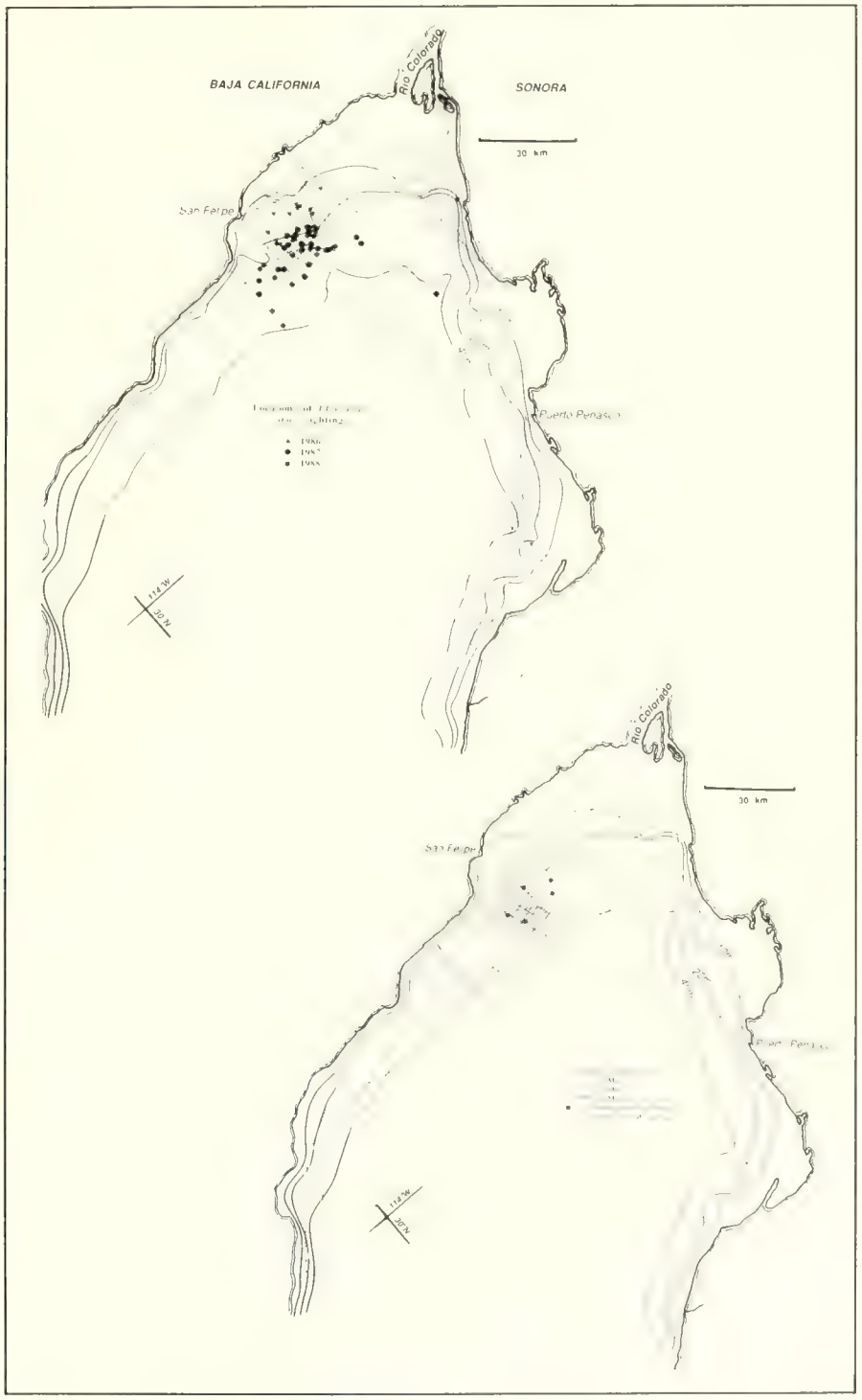

Figure 2
Phocoena sinus sightings and vessel transects conducted in 1986, 1987, and 1988 (top) and aircraft surveys on 3–5 May 1988 (bottom).

($\bar{x}$ 18.3 $\pm$ 6.10 SD; range 2.4–32.2) (Fig. 6, Table 1). Water clarity at sighting locations ranged from 0.9 to 12 m. During four vaquita sightings the boat's depth sounder indicated concentrated layers at 15 (n = 2), 23, and 25 m, possibly representing schooling bait fish or squid upon which the porpoises may have been feeding. On numerous occasions, vaquita surfaced in or alongside surface slicks or long bands of flat water surrounded by rippled water.

Calves represented 9.37% of all individuals. One very young calf was observed on 9 April 1987. It was estimated at <2 days old because of its size, a dorsal fin

Table 1

Summary of all *Phocoena sinus* sightings in the northern Gulf of California, 1986–88. Group sizes are represented by mean, one standard deviation, and range.

Year and dates		Sightings	Distance to shore (km)	Depth (m)	Water temperature (°C)	Water clarity (m)
1986	N	16	16	16	12	12
2 Feb.–27 Mar.	$\bar{x}$	1.7	14.3	21.0	21.5	2.4
	SD	0.87	4.50	5.00	1.83	0.81
	Range	1–4	2.4–20.0	13.5–25.0	17.0–23.0	0.9–4.0
	Est. total ind.	27				
1987	N	22	22	22	12	13
8 Apr.–7 May	$\bar{x}$	2.1	19.3	27.5	22.9	8.2
	SD	1.57	5.71	4.73	2.09	2.46
	Range	1–7	15.3–32.2	20.0–37.0	21.0–26.0	5.0–12.0
	Est. total ind.	46				
1988	N	13	13	13	8	7
21 Mar.–5 May	$\bar{x}$	1.8	20.7	29.5	19.2	4.1
	SD	1.01	6.58	5.87	0.46	1.07
	Range	1–4	7.0–29.0	22.0–40.0	18.5–20.0	2.5–6.0
	Est. total ind.	23				
All years	N	51	51	51	32	32
	$\bar{x}$	1.9	18.3	25.7	21.5	5.0
	SD	1.24	6.10	6.36	2.23	3.10
	Range	1–7	2.4–32.2	13.5–40.0	17.0–26.0	0.9–12.0
	Est. total ind.	96				

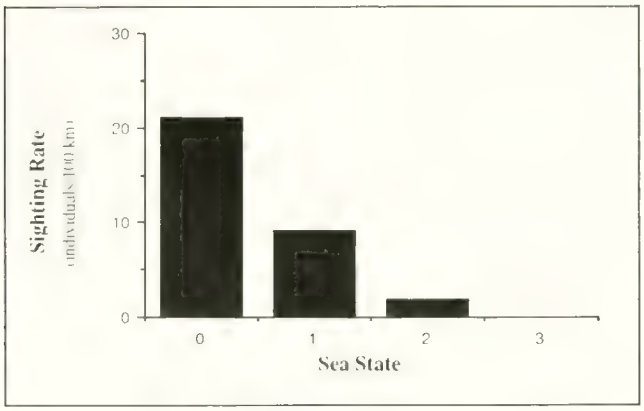

Figure 3
Phocoena sinus sighting rate (individuals/100 km) relative to sea state.

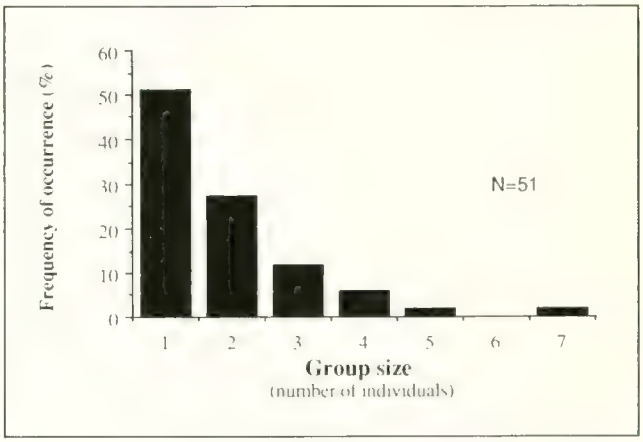

Figure 4
Phocoena sinus group size.

that was not yet fully erect, and the ungainly manner in which it lifted its head from the water with each surfacing.

Aerial surveys

Eleven *Phocoena sinus* (five sightings) were seen during aircraft surveys. All aerial sightings took place between San Felipe and Rocas Consag, and none occurred farther south along the Baja peninsula coast (Fig. 2b), although much less effort was dedicated to this area in relation to the extreme upper Gulf. The number of aircraft surveys was relatively small and non-random. Nonetheless, they served to support *P. sinus* distribution patterns observed during vessel surveys, failed to yield sightings south of the area surveyed by vessel, and illustrated the utility of aircraft as a platform of observation in future study and census of the species.

Sympatric vertebrates

Other marine vertebrates were seen near *P. sinus*;

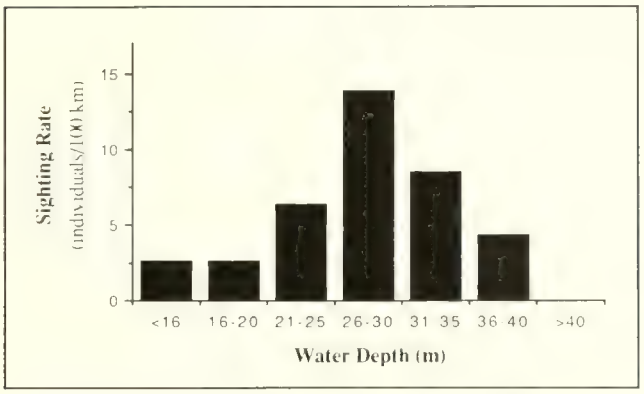

Figure 5
Phocoena sinus sighting rate (individuals/100 km) relative to water depth.

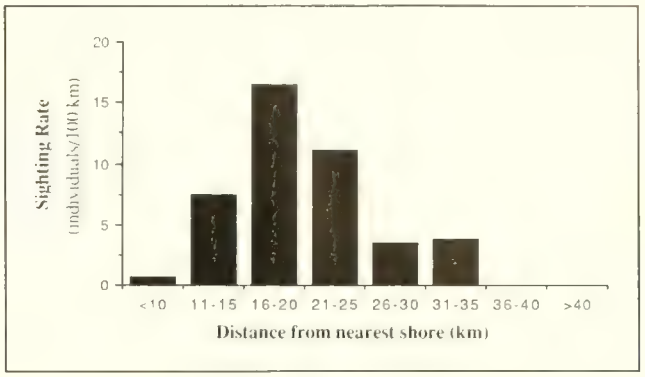

Figure 6
Phocoena sinus sighting rate (individuals/100 km) relative to distance from nearest shore.

affiliations that probably represent utilization of a similar habitat by two or more species rather than active association. Twice, Bryde's whales *Balaenoptera edeni* were seen <1 km from *P. sinus*, and three times common dolphins *Delphinus delphis* were observed <1.5 km from the porpoise. Numerous times black storm-petrels *Oceanodroma melania* and Bonaparte's gulls *Larus philadelphia* dipped into the wake of surfacing vaquita. Manta rays *Manta birostris* were seen once near porpoises.

In addition to vaquita, five other marine mammal species were common within the study area, including bottlenose dolphins *Tursiops truncatus*, common dolphins, fin whales *Balaenoptera physalus*, Bryde's whales, and California sea lions *Zalophus californianus*. There appeared to be a general segregation by location and water depth among the three most common odontocet species. The distribution of *P. sinus* overlapped that of *Delphinus* and *B. edeni*, but not that of *Tursiops* and *B. physalus* (Silber et al. In prep.). Bottlenose dolphins were consistently seen in more shallow water than were vaquita, and common dolphins were generally seen in greater, but comparable, water depths as vaquita. Data on sympatric marine mammals will be presented in greater detail elsewhere (Silber et al. In prep.).

Unconfirmed sightings and fishermen interviews

In February and April 1983 cetaceans that may have been *P. sinus* were seen near Cerralvo Island (24°10′N; 109°55′W) by a scientist who has extensive experience with marine mammals and Gulf of California fauna (G. Notarbartolo di Sciara, Piazza Duca d'Aosta 4, 20124 Milano, Italy, pers. commun., May 1984). In both sightings, the animals were 10–50 m from the observer. They were described as being small, possibly possessing a blunt rostral profile, and surfacing "unobtrusively" in small groups. They were "quite distinct from *Tursiops*, *Delphinus*, or *Lagenorhynchus*" (G. Notarbartolo di Sciara, pers. commun., May 1984). If true, these unconfirmed sightings occurred in an area >850 km south of our southernmost sightings, and extend the present known range considerably.

Based on these observations, the decision was made to interview fishermen in the southern Gulf about the presence of vaquita. In 1987, 17 fishermen from La Paz were interviewed about their fishing practices and their knowledge of the vaquita (Table 2). In most cases the fishermen had spent considerable time on the water (fishing 4–6 days/week, 3–12 months/year, for 5–51 years; $\bar{x} = 20.6$ yrs). Fishermen in the La Paz area generally had no knowledge of vaquita; however, one man was familiar with the porpoise and indicated that he had seen it several times near San Jose Island (25°00′N; 110°40′W), 80 km north of La Paz. Unlike others interviewed, this man was one of two who had been fishing for over 50 years and he had worked in an area (the coast near San Jose Island) different from the other fishermen. In addition, his knowledge of the natural history of marine mammals was regarded as being accurate by the interviewer (D. Aurioles, Centro de Investigaciones, Biologicas B.C.S., APO Postal 128, La Paz, Baja California Sur, México, pers. commun., June 1987). One fisherman described netting near San Jose Island a small cetacean that had rounded ("acorn-like") teeth, a feature characteristic of the genus *Phocoena*.

All fishermen interviewed in San Felipe ($n = 7$) expressed a knowledge of vaquita, and two said that they had entangled the porpoise while fishing for totoaba. Although taking totoaba is illegal, three men indicated that they continue to use gillnets for totoaba.

Table 2

Summary of interviews with fishermen in La Paz, Baja California Sur, and San Felipe, Baja California Norte, regarding fishing practices and knowledge of *Phocoena sinus*.

		San Felipe	La Paz
Number fishermen interviewed		7	17
Distance from home port (km)	$\bar{x}$	37.4	37.8
	SD	39.48	22.32
	Range	1–100	5–112
Number of years engaged in fishing	$\bar{x}$	17.8	23.4
	SD	12.50	15.51
	Range	6–35	5–51
Type of fishing		Gillnet, longline, hook-and-line	Longline, gillnet, trawl, diving
Target species		Shrimp (n = 6) Totoaba (n = 3) Shark (n = 2) Marlin (n = 1) Dorado (n = 1) Yellowtail jack (n = 1)	Spanish mackerel (n = 14) Shark (n = 9) Pacific manta (n = 1) Snapper (n = 1) Striped mullet (n = 1)
Fishing effort		12 mo/yr (n = 4) 3 mo/yr (n = 3)	12 mo/yr (n = 11) 10 mo/yr (n = 1) 3–6 mo/yr (n = 3)
Recognition of photos of *P. sinus*		Yes (n = 7)	Yes (n = 1); No (n = 16)
Estimated total porpoises killed		3–4	0
Common names used		Cochito, cochinito, and vaquita = *P. sinus*	Vaquita = *Kogia* or *Phocoena* spp. Duende = *Lagenorhynchus* Cochinito = *Delphinus* Cochito = *Globicephala*

The vernacular name for *P. sinus* tended to vary between communities and individuals. Fishermen in San Felipe referred to *P. sinus* as "cochito," "cochinito," and "vaquita." In contrast, for La Paz fishermen "vaquita" refers to *Kogia simus* or *Phocoena* spp., whereas "cochinito" refers to *Delphinus delphis*, "cochito" to *Globicephala macrorhynchus*, and "duende," also meaning *P. sinus* in some communities (Magatagan et al. 1984), refers to *Lagenorhynchus obliquidens* (D. Aurioles, pers. commun., June 1987).

Discussion

Although surveys were conducted throughout the upper Gulf, sightings of *Phocoena sinus* were limited almost entirely to the western side. One or a combination of the following features may account for vaquita distribution patterns in the upper Gulf. Relative to the eastern shore, the western boundary exhibits lower surface temperatures (Robinson 1973) resulting partly from northward-bearing upwelled water from the Midriff Island region. With respect to the eastern coastline of the upper Gulf, the western perimeter is characterized by stronger north-south tidal currents yearround (Hendrickson 1973) which may contribute to increased mixing on the west coast.

Vaquita often surfaced near surface slicks, which are caused by tidally induced internal waves (Ewing 1950, Shanks 1983) or areas of convergence of different water masses, a common feature of the northern Gulf of California (Hendrickson 1973, Lepley et al. 1975). Surfacing near slicks has been noted in other cetaceans, including *Feresa attenuata*, *Steno bredanensis*, and *Pseudorca crassidens* (K.S. Norris, Cent. Mar. Stud., Univ. Calif., Santa Cruz, CA 95064, pers. commun., Aug. 1987). Concentrations of small marine organisms are associated with internal waves (Shanks 1983, 1988; Kingsford and Choat 1986). Vaquita and other cetaceans may be drawn to aggregated prey in these features.

It is believed by some researchers that the entire *P. sinus* population is limited to the upper Gulf, which represents the smallest range of any marine cetacean (Brownell 1986, Barlow 1986); however, the actual range remains unsubstantiated. Although presently

untested, I suggest that vaquita occur in the upper Gulf year-round, and although the majority of the population may have receded to the upper Gulf following a relatively recent decline in population size, some individuals are probably scattered throughout the Gulf as separate subpopulations or a sparsely dispersed single population. Reported sightings of *P. sinus* outside the northern Gulf (Scammon 1874, Norris and McFarland 1958, Norris and Prescott 1961, Villa-R. 1976; presented here) suggest the possibility of a greater historical range. However, extensive field work on cetaceans near the Midriff Islands, Guaymas, and Kino Bay areas has not yielded sightings of vaquita (L. Ballance, Dep. Biol., Univ. Calif., Los Angeles, CA 90024, pers. commun., May 1989; L.T. Findley, Escuela de Ciencias Marítimas y Alimentarias, Instituto Tecnológico y de Estudios Superiores de Monterrey, Unidad Guaymas, A.P. 484, Guaymas, Sonora, 85400 México, pers. commun., Nov. 1985; B. Tershy, Dep. Biol., Cornell Univ., Ithaca, NY 14853, pers. commun., Sept. 1987). Most phocoenids are cold-temperate water animals (Gaskin 1982), with ranges restricted to <20°C. Northern Gulf of California surface water temperatures in the summer and fall can exceed 28°C (Hendrickson 1973, Robinson 1973). If the porpoise is limited to this region, it deviates remarkably from other phocoenids in its ability to tolerate seasonal water temperature fluctuations.

Management recommendations

Exposure of the depleted *P. sinus* population to current levels of human impact may result in the demise of the species. Habitat degradation and pesticide contamination of the northern Gulf may contribute to the decline of *P. sinus*. However, vaquita mortality in gillnets (Brownell 1983, Robles et al. 1986, Silber 1988) may represent the most direct threat to the population, and increased efforts to reduce porpoise entanglement is imperative. Nets set for totoaba probably account for the highest percentage of incidental porpoise deaths. The totoaba is an endangered species and cannot be legally caught, sold, or exported. Nonetheless, illegal fishing continues due to the inability to enforce restrictions. Additional study is needed to quantify incidental mortality rates and to explore possible modifications of fishing amounts, timing, and technique. Vaquita sightings occurred predominantly in discrete locations and water depths. If widespread fishing bans are not possible, emphasis should be placed on excluding fishing from these areas. However, because maximum catch of totaba also occurs in spring (Flanagan and Hendrickson 1976), there will be difficulty achieving compliance by fishermen. Rigorous sanctions on importation of totoaba bound for U.S. markets are required. Additional boat and aircraft census surveys should be conducted to determine the vaquita population size, and to enhance current knowledge of the ecology of the porpoise. Large areas of the northern Gulf have been recommended for consideration as a Marine Sanctuary (B. Villa-R., Inst. Biol., Univ. Nal. Autón. México, A.P. 70-153, México, D.F. 04510, pers. commun., Feb. 1986), and these plans should be endorsed. Mexican and U.S. scientists should engage in joint efforts to monitor changes in the vaquita population size. Action by Mexican and U.S. governments, fishing cooperatives, cetacean biologists, and resource management personnel is necessary to the preserve the species.

Acknowledgments

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Incidental Take of Marine Mammals in Foreign Fishery Activities Off the Northeast United States, 1977–88

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Abstract. – Fishery observers aboard foreign commercial fishing vessels collected information on the incidental catch of marine mammals in the Exclusive Economic Zone (EEZ) off the northeastern United States since March 1977. Observer coverage on foreign vessels was 25–35% during 1977–82, and increased to 58%, 86%, 95%, 98%, 100%, and 100%, respectively, in 1983–88. During 1981–88, observers have covered most joint-venture fishing operations. During 1977–88, observers reported 538 marine mammals captured incidental to direct and joint-venture fishing activities. Eight cetacean species and three unidentified baleen whales were caught, principally in the fisheries for Atlantic mackerel *Scomber scombrus*, and squid *Illex illecebrosus* and *Loligo pealei*. Pilot whales *Globicephala* spp. (297/538) and common dolphins *Delphinus delphis* (203/538) comprised 93% of the catch. Chi-square tests indicate that significant differences in diel rates of capture occurred between the two species. The number of *Globicephala* spp. captured at night (2000–0400 h) in the Atlantic mackerel fishery was significantly less ($\chi^2 = 8.28$, $P < 0.03$) than the number caught during day (0800–1600 h) or dawn/dusk (1600–2000 h, 0400–0800 h). The number of *D. delphis* captured during daylight in the *Loligo* squid fishery was significantly less ($\chi^2 = 44.48$, $P < 0.001$) than the number caught at night or dawn/dusk. A minke whale *B. acutorostrata* (released alive) and individuals of two endangered species, a humpback whale *Megaptera novaeangliae* (released alive) and a right whale *Eubalaena glacialis*, were also captured incidental to fishing activity. During December 1986–February 1988, observers collected whole, dead, non-endangered mammals for detailed shoreside examination. Trawl contents at the time of capture and subsequent analysis of mammal stomach contents suggest that *L. pealei* is a major component of the mid-shelf and shelf-edge diet of common dolphins and pilot whales. Further, pilot whales, considered principally as teuthophagous, were observed to selectively feed on mackerel while on the Continental Shelf.

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Marine mammal/fishery interactions in United States waters have received widespread attention in recent years (Bonner 1982, Fowler 1982, Lowry 1982, Loughlin et al. 1983, Loughlin and Nelson 1986). These interactions, generally involving commercial fisheries (Mate 1980), are of two types: (1) direct or operational, and (2) indirect or ecological (Lowry 1982).

In the shelf waters off the northeastern United States, marine mammal/commercial fishery interactions have been described only for fisheries occurring in nearshore waters (Gilbert and Wynne 1985). These interactions occur in the fixed-gear fisheries for American lobster *Homarus americanus*, the surface-gillnet fishery for Atlantic herring *Clupea harengus* and Atlantic mackerel *Scomber scombrus*, and the groundfish-gillnet fishery for assorted finfish, principally Gadidae and Pleuronectidae. Two principal marine mammals taken incidentally in these fisheries are the harbor porpoise *Phocoena phocoena* and the harbor seal *Phoca vitulina*. The gray seal *Halichoerus grypus* is infrequently captured. These three species are known to feed on fish caught in nets and to become entangled, thereby damaging fishing gear.

Marine mammal/fishery interactions in the deeper, offshore waters off the northeastern United States have not been previously documented. Under the provisions of the United States Marine Mammal Protection Act (MMPA) of 1972 a General Permit system was established by the National Marine Fisheries Service (NMFS) allowing incidental taking of marine mammals in commercial fishing operations. All domestic and foreign fishing vessels were required to have a valid permit on board that established an allowable limit on the number of non-endangered marine mammals that could be taken within a specified fishery (i.e., mackerel, squid). The Magnuson Fishery Conservation and Management Act of 1976 as amended in 1983, (MFCMA, Public Law 94-265) mandated the placement of Fisheries Compliance Inspectors, or observers,

beginning in 1984, on 100% of all foreign fishing vessels operating within the 200-mile outershelf and slope waters off the United States. (This area is further referred to as the Exclusive Economic Zone, or EEZ). Since that time in 1984, reporting of marine mammal takes incidental to foreign fishing activities has been more effectively monitored by species and fishery.

In this paper we summarize the observed incidental take of marine mammals from all foreign fishing activities that operated within the EEZ off the northeastern United States from 1977 to 1988. The incidental take of common dolphins *Delphinus delphis* and of pilot whales *Globicephala* spp.*, the two most frequently caught species, are examined relative to the type of fishery in which they were taken, the nationality involved in the fishery operation, and the time of the incidental take (day versus night). Morphological measurements, sex, and stomach contents for 33 of the common dolphins taken during 1986 and 1988 are also reported in this study. These measurements and records are the first such information taken from any marine mammal specimens recently killed in the waters off the northeastern United States.

Summary of foreign fisheries

Fishing operations

Large-scale foreign fishing activity began off the U.S. east coast in the early 1960s with the arrival of the distant-water fleet (DWF) from Europe and Japan. Initially, the DWF harvested groundfish (Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, hakes, flounders, etc.) and pelagics (Atlantic herring and Atlantic mackerel) (Brown and Halliday 1983). Declining fish stocks, coupled with management measures implemented in the late 1960s, under the auspices of the International Commission for the Northwest Atlantic Fisheries, resulted in the DWF shifting emphasis to "under-utilized" species, such as long-finned squid *Loligo pealei*, short-finned squid *Illex illecebrosus*, and Atlantic butterfish *Peprilus triacanthus*.

The MFCMA, which became effective March 1977, significantly altered DWF activities within the EEZ. Fishing effort was immediately reduced, and the number of foreign vessels operating within the east coast EEZ declined from a high of 161 vessels in 1977 to 26 in 1988. From 1977 through 1982, an average of 120 different foreign vessels per year (range 102–161) operated within the EEZ. In 1982, there were 112 different foreign vessels; 16%, or 18, were Japanese tuna longline vessels operating off the east coast. The Northeast Region Observer Program assumed responsibility for observer coverage of the east coast Japanese tuna longline fishery in 1982. This fishery has been conducted from the Canadian boundary-line south to Florida and, prior to 1982, in the Gulf of Mexico. In 1983, a decrease in the total allowable catch allocated to each foreign country fishing off the east coast resulted in fewer foreign vessels operating within the EEZ. Between 1983 and 1988, the numbers of foreign vessels operating within the EEZ each year were 67, 52, 62, 33, 27, and 26, respectively. Observer coverage (the ratio of observer coverage days to the number of foreign fishing days) ranged from 25 to 35% for the period 1977–82. Coverage increased steadily since 1982, and was maintained at 58%, 86%, 95%, 98%, 100%, and 100% in 1983-1988, respectively.

Since 1977, fourteen nations have been given catch allocations to operate off the east coast within the EEZ. Direct fishing (DWF catching and processing their own catches) was limited to five Outer Continental Shelf locations referred to as fishery windows (Fig. 1) and to specified times of year. From 1977–83, the DWF led by Italy, Spain, and Japan principally targeted long-finned and short-finned squid within these windows. Direct squid fishing operations ceased at the end of the 1986 fishing season.

Joint-venture fishing operations (U.S. captains transfer their catches to foreign processing vessels) began in 1981. Squid joint ventures, which were unrestricted areally, were authorized without any associated direct fishing allocations. In 1983 the German Democratic Republic (GDR), and in 1984 the Netherlands, commenced joint-venture operations for Atlantic mackerel off the east coast. Mackerel joint ventures which have been authorized with associated allocations for direct fishing have not been restricted to the fishery windows. In 1988, Poland also commenced commercial fishing operations for Atlantic mackerel that included joint-venture and direct fishing. Prior to 1988, Poland conducted a research fishery each year between 1981 and 1987 for Atlantic mackerel that involved Polish catching/processing vessels staffed with Polish and U.S. fishery data collectors.

Foreign vessels engaged in *Loligo* and *Illex* squid fishing operations used off-bottom trawls, and did not utilize squid attracting devices, such as lights, during night-time fishing. In the Atlantic mackerel fishery, both off-bottom high-opening trawls and pelagic trawls

*The distribution of the Atlantic pilot whale *Globicephala melaena*, the northern species, overlaps with the short-finned pilot whale *G. macrorhyncha*, mainly a southern species, between about 35°30'N to 38°00'N (Leatherwood et al. 1976). Although, *G. melaena* is the most common and the most likely taken in the DWF foreign fisheries, there is a possibility that the southern species might also be occasionally taken. Therefore, in this paper both pilot whales are considered together.

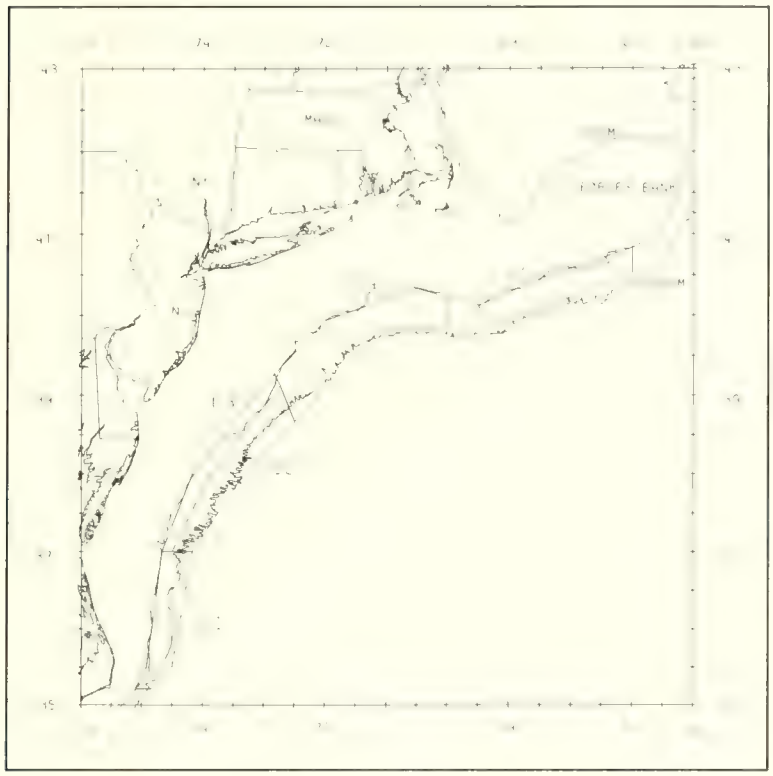

Figure 1
Foreign fishery windows within the EEZ off the northeastern United States.

have been used; currently the DWF utilizes several different pelagic trawls.

Principal target species

Loligo or long-finned squid

Although *Loligo* occurs from the Gulf of Mexico north to New Brunswick, Canada (Summers 1967), the distribution of long-finned squid (hereafter referred to as *Loligo*) is primarily from Cape Hatteras, North Carolina, to Georges Bank and into the Gulf of Maine (Lange 1980). *Loligo* overwinters along the shelf edge from Cape Hatteras to Georges Bank at water temperatures generally >8°C (Lange and Sissenwine 1980). During spring and summer *Loligo* moves into nearshore waters to spawn (Summers 1967). Commercial concentrations are found primarily off southern New England and the mid-Atlantic regions from about Georges Bank to Baltimore Canyon (Lange 1980, Lange and Johnson 1981). DWF fishing prior to the MFCMA occurred at depths of 100–500 m along the shelf edge from November through March (Lange 1980), but since 1977 fishing operations have been restricted in area and season. Since 1987, the allocation for *Loligo* has been reduced strictly to bycatch in the Atlantic mackerel fishery; therefore, DWF *Loligo* fishing has been suspended.

Illex or short-finned squid

The short-finned squid (hereafter referred to as *Illex*) is a more northern species than *Loligo*, ranging from Florida to Newfoundland (Squires 1957). In late autumn (October–December), *Illex* moves offshore toward the shelf edge and beyond (Lange and Sissenwine 1980). Spawning is believed to occur offshore at great depths, primarily from December to March (Lange and Sissenwine 1980). During warmer months *Illex* move nearshore to feed (Lange 1980). Commercial concentrations occur from the mid-Atlantic, near Baltimore Canyon, to Newfoundland (Lange and Johnson 1981). The DWF *Illex* fishery took place from June through October, while this species is on the shelf (Lange 1980). In 1987, *Illex* allocations for DWF fisheries were suspended. At present, there is no direct foreign fishing effort for this species.

Atlantic mackerel

Atlantic mackerel, a major target species of the DWF, overwinter along the edge of the continental shelf between Cape Hatteras and Sable Island, Nova Scotia (Anderson and Paciorkowski 1980). The overwintering population consists of two components (southern and northern), which separate in spring. The southern component moves nearshore in early spring along the

Virginia Capes and proceeds northeastward to spawn off the New Jersey and Long Island coasts from mid-April to early May. By midsummer, the southern component reaches the Gulf of Maine where it remains throughout summer (Anderson and Paciorkowski 1980). Migration out of the Gulf of Maine begins in autumn as the southern component returns to deeper, offshore waters. The northern component migrates further north in spring along the Nova Scotian shelf to the Gulf of St. Lawrence where spawning occurs during June–July (Anderson and Paciorkowski 1980). The northern component begins leaving the Gulf of St. Lawrence in September and returns to the mid-Atlantic region to overwinter.

The seasonal DWF mackerel fishery occurs in the mid-Atlantic region during the winter when both components of the mackerel population concentrate primarily along the shelf edge (Anderson and Paciorkowski 1980), although commercial quantities are sometimes encountered in waters as shallow as 30 m.

Methods and materials

Data collection on incidental take

Observers monitor compliance with applicable fishing regulations, collect biological data and samples, and serve in a liaison role, when needed, between foreign and domestic captains. In the northeast region, observer training is the responsibility of the NMFS Observer Program. Between 1977 and 1985, observers routinely recorded the number of marine mammals taken incidentally in foreign fishing activities. In 1986, a new sampling protocol was implemented to collect additional information on marine mammals, sea turtles, and marine debris. Observers are now required to complete sighting forms, document the circumstances of capture and obtain biological data on incidentally captured marine mammals* and sea turtles. Marine mammal biological sampling includes five straight-line body measurements (e.g., snout to fluke notch, flipper length, flipper width, fluke width, and dorsal fin height), girth at pectorals, sex, and total weight. Additionally, when feasible, incidentally caught marine mammals are frozen whole, brought ashore, and later examined by researchers at the Smithsonian Institution.

Data analysis on incidental take

A paired Mann-Whitney test (Zar 1974) was used to test for differences between the total number of cetaceans killed per day (kill-rate) in the 1984–88 Netherlands and the GDR mackerel fishery. Data for Poland were not included, because that country did not begin commercial fishing until 1988. Because a Mann-Whitney test examines only differences in paired data sets, a Friedman rank sums test (Hollander and Wolfe 1973) was used to examine the kill-rates between Italy, Spain, and Japan in the 1984–86 *Loligo* squid fishery.

Randomly selected samples of 334 trawl logs from the 1985 Atlantic mackerel fishery (from Netherlands) and 1018 trawl logs from the 1985 *Loligo* squid fishery (from Italy) were used to determine the expected level of fishing effort (number of tows) for each of three time periods—Day (0800–1600), Dawn/Dusk (0400–0800 and 1600–2000), and Night (2000–0400)—within each fishery. The Chi-Square Statistic was then used to determine whether there were significant differences in the numbers of common dolphins and pilot whales incidentally taken in each fishery (relative to fishing effort) due to time of day of the take.

Data analysis on stomach contents, sex and total length

A total of 95 common dolphins and 169 pilot whales taken between 1986 and 1988 were measured (total standard length) and sexed at sea. Stomach contents from 33 of the common dolphins were examined by Smithsonian Institution personnel, and the information was provided for this paper. Prior to 1986, stomach contents and sex data were not collected.

Results

Observers reported 538 marine mammals incidentally caught during foreign fishing activities in the EEZ off the northeast United States between March 1977 and December 1988 (Table 1). Pilot whales were the most frequently caught marine mammal with 297 caught, representing 55% of the total marine mammal take between 1977 and 1988 (Table 1). Common dolphins were the next most-frequently-taken cetacean with 203 caught, composing 38% of the total incidental takes. Approximately 5% of the total catch consisted of three other members of the Delphinidae: Atlantic white-sided dolphin *Lagenorhychus acutus*, bottlenose dolphin *Tursiops truncatus*, and Risso's dolphin *Grampus griseus* (Table 1).

Six large whales were reported caught or entangled during fishing operations. One subadult or juvenile right whale *Eubalaena glacialis* (based on observer identification and estimated length of 6 m) and one unidentified baleen whale were taken in the *Loligo* fishery. A humpback *Megaptera novaeangliae*, minke

*In this paper, an incidental take is defined as any live marine mammal or any carcass caught during foreign fishing activity.

Table 1

Summary of incidental take of marine mammals as reported by U.S. fisheries observers on foreign vessels in the shelf and slope waters of the northeastern United States. Values in parantheses represent animals released alive. (jv = joint venture)

Year/ Fishery	Country	Common dolphin	Pilot whale	White-sided dolphin	Bottlenose dolphin	Risso's dolphin	Unid. dolphin	Right whale	Humpback whale	Minke whale	Unid. whale	Total
1977–83												
Illex	Italy		1				2					3
	Japan		1									1
	Mexico		1									1
	Spain		3									3
	USA (jv)		6									6
Loligo	Italy	2	2									4
	Japan	1	3				1					5
	Mexico				1							1
	Spain	1	5					1			1(1)	8(1)
Tuna	Japan		2				1		1(1)		1	5(1)
Hake	USSR		2		1						1	4
Mackerel	Poland	4	13		1							18
Totals		8	39		3		4	1	1(1)		3(1)	59(2)
1984												
Illex	USA (jv)		1									1
Loligo	Italy	3	3	2								8
	Spain		7									7
Tuna	Japan					1						1
Mackerel	GDR		1									1
	Netherlands		11									11
	Poland				1							1
Totals		3	23	2	1	1						30
1985												
Loligo	Italy	56	1			1						58
	Japan	1										1
	Spain	4	4				1					9
Mackerel	GDR		8	3								11
	Netherlands	5	32		3							40
	Poland		1									1
	USA (jv)		1									1
Totals		66	47	3	3	1	1					121
1986												
Loligo	Italy	54	1			1						56
	Spain	1										1
	USA (jv)		2									2
Tuna	Japan									1(1)		1(1)
Mackerel	GDR	4	12(1)									16(1)
	Poland	3	1(1)									4(1)
	USA (jv)	14	4									18
Totals		76	20(2)			1				1(1)		98(3)
1987*												
Illex	Italy					1						1
Mackerel	GDR	11	12(1)									23(1)
	Netherlands	7	11									18
	USA (jv)	1	3									4
Totals		19	26(1)			1						46(1)
1988												
Mackerel	GDR	20	27									47
	Netherlands		50	4	1							55
	Poland	11	58(3)	4	1		1					75(3)
	USA (jv)		7									7
Totals		31	142(3)	8	2		1					184(3)
1977–88 Totals		203	297(6)	13	9	4	6	1	1(1)	1(1)	3(1)	538(10)

*Directed foreign *Loligo* fishing operations ceased in 1986.

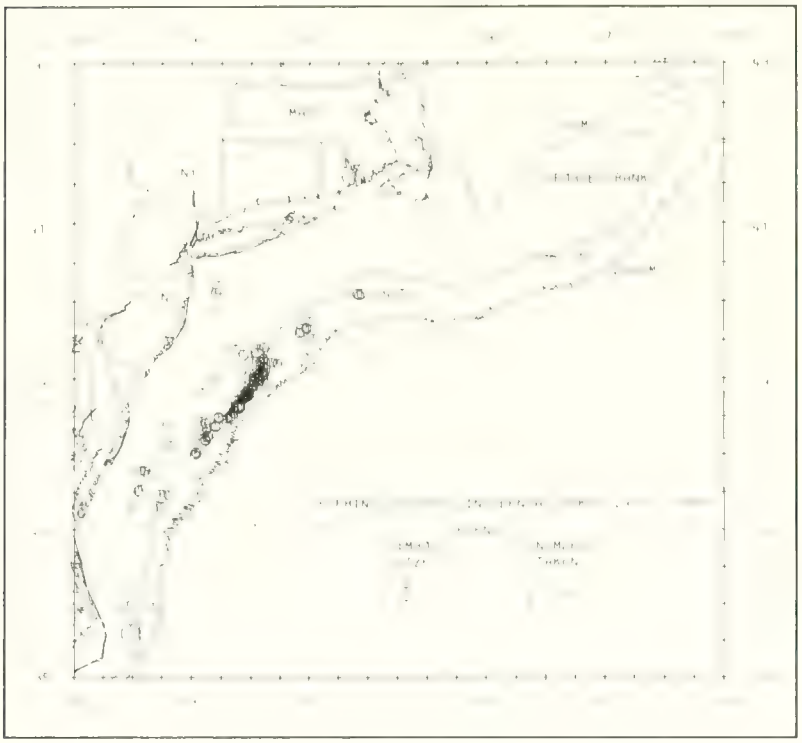

Figure 2
Distribution of incidental takes of common dolphin in foreign fishing activities off the northeastern United States, 1977–88.

Balaenoptera acutorostrata, and an unidentified baleen whale were also reported taken in the tuna longline fishery (Table 1). Another unidentified baleen whale was taken in the hake fishery.

Location of incidental takes of common dolphins and pilot whales

A total of 68% (n = 136) of the common dolphins captured in foreign fishing activities were caught along the shelf edge, represented by the 100-m isobath, between 37°30′N and 40°00′N latitudes (Fig. 2), and 69% (n = 138) of the common dolphins were taken between December and February. Most (n = 152) of the pilot whales captured during foreign fishing activities also occurred along the shelf edge (Fig. 3), and 83% (n = 246) were captured between March and July. Of the total number of pilot whales taken incidentally to fishing, 8% (n = 24) were captured between December and February, as compared with 69% for common dolphins.

Incidental takes by fishery and country

During 1977–83, 54% (32/59) of the incidental bycatch of marine mammals in foreign fishing activities was taken in the *Loligo* and *Illex* fisheries (Table 1). This high percentage is consistent with the distribution of DWF fishing effort during this period. Since 100% observer coverage of most fisheries did not begin until 1984, the number of marine mammals taken during this period is probably under-represented.

***Loligo* and *Illex* fisheries** A total of 61% (n = 123) of the total number of common dolphins taken during 1977–88 (n = 203) were caught in the *Loligo* fishery, and 94% (n = 116/123) of these takes occurred during 1985–86. Again, takes prior to 1984 were probably under-represented. Italian vessels caught 93% of the common dolphins taken in the *Loligo* fishery.

The total number of pilot whales caught in the *Loligo* fishery (n = 28) was 9.4% of the total number of pilot whales taken incidentally to all foreign fishing activities. Of the pilot whales taken in the *Loligo* fishery between 1984–86, 61% (n = 11/18) were taken by Spain.

No common dolphins were taken in the *Illex* fishery; however, 13 pilot whales were taken between 1977 and 1984. Of the pilot whales taken, 46% (n = 6) were caught by U.S. joint-venture vessels.

Atlantic mackerel fishery During 1984–88, 76 common dolphins were taken in the fishery for Atlantic mackerel (Table 1). Of the common dolphins taken in this fishery, 46% (n = 35/76) were caught by GDR vessels, 19% (n = 15) by U.S. joint-venture vessels, 18% (n = 14) by Polish vessels, and 17% (n = 12) by Dutch vessels.

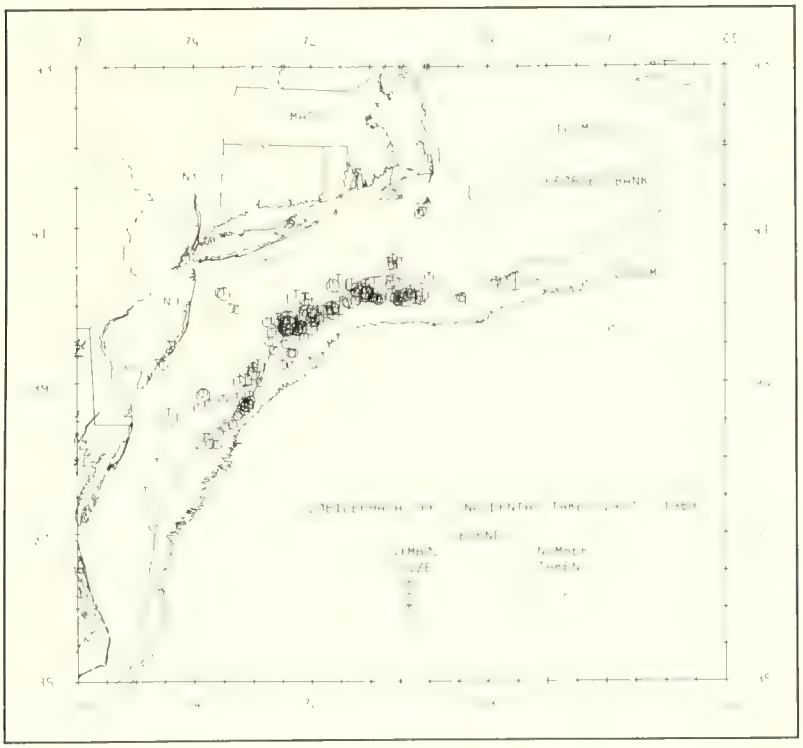

Figure 3
Distribution of incidental takes of pilot whales in foreign fishing activities off the northeastern United States, 1977–88.

Of the DWF fisheries mortality of pilot whales since 1984, 93% occurred in the Atlantic mackerel fishery (Table 1). During 1984–87, the Netherlands and the GDR caught 54 and 33 animals, respectively, which combined represent 90% ($n = 97$) of the pilot whales taken in the mackerel fishery during that 4-year period. In 1988, Poland began commercial fishing for Atlantic mackerel and caught 41% ($n = 58$) of the pilot whales taken that year. Although the Netherlands did not fish in the EEZ during 1986, they still caught 44% (104/239) of the pilot whales taken since 1984 in the Atlantic mackerel fishery.

Summary of kill rates by fishery and country

***Loligo* fishery** The total number of marine mammals (all species) killed per days fished (k/d rate) by Italy in the directed *Loligo* fishery was more than six times that of either Japan or Spain between 1984 and 1986 (period of nearly 100% observer coverage) (Table 2). During the years 1985 and 1986, this rate was approximately 10 times greater than the same rate for Spain, in spite of comparable number of days fished (Table 2). The k/d rates for 1984–86 between the three countries, however, are not significantly different using the Friedman test ($P<0.19$).

Atlantic mackerel fishery The k/d rate in the Atlantic mackerel fishery has varied both over years and among countries (Table 3). Between 1984 and 1988, the average kill rate for the GDR and the Netherlands was 0.12 k/d. The Netherlands annual k/d rates were 4 to 17 times greater than GDR rates, and differences in the k/d rates between these two countries are significant, $P<0.06$. With the inclusion of the 1988 takes by Poland, the all-years (pooled) k/d rate increases to 0.14 (Table 3). The 1988 k/d rates for each country were the highest observed during the 5-year period, 1984–88 (Table 3).

Summary of incidental take by fishery and time of day

***Loligo* fishery** The incidental take of common dolphins during daylight hours (0800–1600) was significantly less ($\chi^2 = 44.48$, 2 df, $P<0.001$) than the number captured during dawn/dusk or the night (Table 4). The number of pilot whales captured in the *Loligo* fishery did differ significantly by time period ($\chi^2 = 1.02$, 2 df) (Table 4).

Atlantic mackerel fishery Similar to the *Loligo* fishery, the number of common dolphins captured during daytime hours was significantly less ($\chi^2 = 20.42$, 2 df, $P<0.001$) than the number caught in tows at other time periods throughout the day (Table 5). The number of pilot whales caught in tows conducted during the night (2000–0400) was significantly less ($\chi^2 = 8.28$, 2 df,

Table 2

Numbers of cetaceans killed and days fished by Italy, Japan, and Spain while *Loligo* squid fishing off the northeastern United States, 1984–86. Numbers do not include animals captured and released alive.

	1984			1985			1986			Total		
	days	kill	k/d	days	kill	k/d	days	kill	k/d	days	kill	k/d
Italy	1000	8	0.01	631	58	0.09	524	56	0.11	2155	122	0.06
Japan	267	0	0	73	1	0.01	26	0	0	366	1	<0.01
Spain	678	7	0.01	936	9	0.01	511	1	<0.01	2125	17	0.01
Total	1945	15	0.01	1640	68	0.04	1061	57	0.05	4646	140	0.03

Table 3

Numbers of cetaceans killed and days fished by German Democratic Republic (GDR), Poland, and Netherlands while Atlantic mackerel fishing off the northeastern United States, 1984–88. Numbers do not include animals captured and released alive.

	1984			1985			1986			1987			1988			Total		
	days	kill	k/d	days	kill	k/d	days	kill	k/d	days	kill	k/d	days	kill	k/d	days	kill	k/d
GDR	166	1	0.01	213	11	0.05	306	15	0.05	415	22	0.05	344	47	0.14	1444	96	0.07
Poland*	—	—	—	—	—	—	—	—	—	—	—	—	306	72	0.24	306	72	0.24
Netherlands	65	11	0.17	131	40	0.31	0	0	0	94	18	0.19	95	55	0.58	385	124	0.32
Total	231	12	0.05	344	51	0.15	306	15	0.05	509	41	0.08	745	173	0.23	2135	292	0.14

*Does not include scientific research.

Table 4

Observed and expected catch by time of day of common dolphins and pilot whales taken in the 1977–86 *Loligo* squid fishery off the northeastern United States.

Time of day*	Observed frequency	Expected frequency	χ^2
Common dolphins			
0800–1600	11	46	26.63
2000–0400	57	35	13.83
0400–0800			
1600–2000	55	42	4.02
$\chi^2 = 44.48$, 2 df			
$P < 0.001$			
Pilot whales			
0800–1600	11	9	0.444
2000–0400	5	7	0.571
0400–0800			
1600–2000	9	9	0.000
$\chi^2 = 1.015$, 2 df			
$P < 0.6017$, ns			

*Day (0800–1600), night (2000–0400), dawn/dusk (0400–0800, 1600–2000).

Table 5

Observed and expected catch by time of day of common dolphins and pilot whales taken in the 1984–88 Atlantic mackerel fishery off the northeastern United States.

Time of day*	Observed frequency	Expected frequency	χ^2
Common dolphins			
0800–1600	7	25.7	13.610
2000–0400	36	25.7	4.130
0400–0800			
1600–2000	34	25.7	2.680
$\chi^2 = 20.42$, 2 df			
$P < 0.001$			
Pilot whales			
0800–1600	91	80	1.510
2000–0400	59	80	5.510
0400–0800			
1600–2000	90	80	1.250
$\chi^2 = 8.28$, 2 df			
$P < 0.03$			

*Day (0800–1600), night (2000–0400), dawn/dusk (0400–0800, 1600–2000).

Table 6

Summary of stomach contents of 33 common dolphins killed in foreign fishing activities off the northeastern United States, 1986–88.

TL (cm)	Sex	Stomach content: Weight (kg)	Stomach content: Description	Fishery
195	M	1.17	Partial digested squid, few fish bones	Squid
205	M	0.48	Partly digested squid pens and beaks, a few hake otoliths	Squid
194	M	0.27	~50 cc squid beaks and pens, no fish remains	Squid
226	M	3.38	Mostly whole squid and some well-digested fish	Squid
205	M	0.89	1 L digested fish and 8–11 pairs of squid beaks	Squid
180	F	0.19	Squid	Squid
208	M	No data	No data	Squid
190	M	0.99	Squid	Squid
207	M	0.28	Squid	Squid
210	F	Empty		Squid
193	M	2.68	4 intact mackerel, a few squid beaks and pens, and two unknown fish	Mackerel
188	M	0.16	Few fish vertebrae and squid pens and beaks	Mackerel
209	M	2.20	No data	Mackerel
199	M	1.99	3 partially digested mackerel, squid beaks and pens	Mackerel
193	M	0.91	3/4 L fish bones, few small squid beaks	Mackerel
200	M	1.18	1 intact mackerel, 1 partly digested mackerel, no squid parts	Mackerel
202	M	No data	3/4 L fish including 3 whole mackerel and 2 pairs of squid beaks	Mackerel
196	M	2.15	6–7 intact mackerel and some squid beaks	Mackerel
200	M	1.90	1.5 L partially digested fish and 3 pairs of squid beaks	Mackerel
194	F	2.8	6 mackerel, 4 whole squid	Mackerel
188	F	1.34	Mackerel in fore stomach, squid pen in pyloric	Mackerel
203	M	1.81	3 mackerel (33 cm SL) and 2–3 well-digested mackerel	Mackerel
207	M	1.94	Mackerel	Mackerel
208	M	1.34	Mackerel	Mackerel
223	M	4.2	16 mackerel (30 cm SL) in main stomach, trace squid in pyloric	Mackerel
190	F	0.15	Trace squid	Mackerel
198	F	1.86	Squid and 1 mackerel (30 cm)	Mackerel
214	M	3.83	14 mackerel (25–38 cm SL)	Mackerel
216	M	1.21	Mackerel	Mackerel
205	M	3.04	Mackerel	Mackerel
216	M	3.86	7 mackerel (35 cm), and equal volume of digested mackerel	Mackerel
195	F	1.87	No data	Mackerel
204	F	1.99	Mackerel in fore stomach	Mackerel

$P<0.03$) than the number of pilot whales caught during the day or dawn/dusk (Table 5).

Food habits and morphometrics based on examination of animals collected in DWF fisheries

Food habits Stomach contents of 17 common dolphins taken in the mackerel fishery and 10 taken in the *Loligo* fishery reflected the target species of the respective fisheries (Table 6). Nine of the stomachs examined from dolphins taken in the Atlantic mackerel fishery contained only Atlantic mackerel. Eleven of the stomachs contained mixed fish (Atlantic mackerel and/or unidentifiable parts) and squid. One of the stomachs contained only squid. Data were not recorded for two stomachs. Examination of two stomachs taken from pilot whales caught in the Atlantic mackerel fishery contained only Atlantic mackerel.

In comparison, 4 of the 10 stomachs examined from dolphins taken in the *Loligo* fishery contained only unidentifiable squid parts. Four other stomachs contained squid spp. and unidentifiable fish parts. One stomach was empty and data were not reported for one stomach.

Morphometrics The sex ratio of the 95 common dolphins measured at sea during 1986–88 was 52 males, 22 females, and 21 not determined (70.3% male). These animals ranged in size from 150 to 290 cm (Fig. 4). The size range for males was 150–290 cm ($\bar{x}$ 209 cm), 185–260 cm ($\bar{x}$ 202 cm) for females. Of the dolphins measured, 33 were <200 cm in length. This places them in the prepubescent length-category provided by Collett and Saint-Girons (1984).

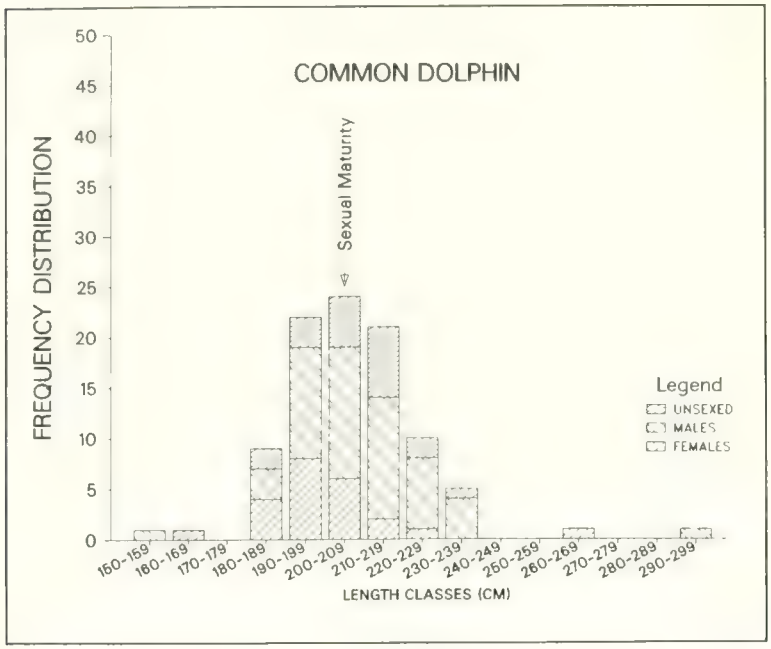

Figure 4
Length distribution of incidentally captured common dolphins measured by observers aboard foreign fishing vessels off the northeastern United States, 1986–88. Size at attainment of sexual maturity is from Perrin and Reilly (1984).

A total of 169 pilot whales measured during 1986–88 included 104 females, 40 males, and 25 not determined (72.2% female). These animals ranged in size from 199 to 510 cm (Fig. 5). Of the females, 85% (n = 88) measured 366–510 cm ($\bar{x}$ 429 cm), which is greater than the average length at attainment of sexual maturity (365 cm) as reported for *G. melaena* in the western North Atlantic by Perrin and Reilly (1984). The size range for the males was 199–470 cm ($\bar{x}$ 325 cm). No males recorded by observers reached the average length at attainment of sexual maturity (490 cm) reported by Perrin and Reilly (1984).

Discussion

Distribution of common dolphins and pilot whales relative to timing and location of take

The location (Figs. 2, 3) and timing of the incidental take (midwinter to late spring) of these two species are directly related to the seasonal distribution of each species. From mid-January to May, the distribution of common dolphins generally extends from Cape Hatteras northeastward to Georges Bank in mid- to outershelf waters (Hain et al. 1981, CETAP 1982, Payne et al. 1984). During mid- to late summer, many common dolphins move northward out of the EEZ onto the Scotian Shelf (Sergeant 1958, Sergeant and Fisher 1957) before returning southward to Georges Bank during late fall and winter. Therefore, the distribution of this species is most restricted during midwinter and early spring in the mid-Atlantic, coincident to the DWF *Loligo* and Atlantic mackerel fisheries.

Likewise, pilot whales are also distributed along the outershelf of the mid-Atlantic and southern New England waters of the EEZ during midwinter and spring (December–May). Throughout spring and early summer, pilot whales move northward along the shelf-edge and by summer–late fall their distribution is most widespread throughout the EEZ (CETAP 1982, Payne et al. 1984). Pilot whales were taken when their distribution was most concentrated along the southern New England shelf-edge in spring.

Incidental take by fishery and country

A large percentage of common dolphins were taken by Italy during *Loligo* squid fishing operations. This occurred despite reduction of Italian allocation and effort (i.e., days fished) in the *Loligo* fishery during 1985 and 1986. The Netherlands took a large percentage of pilot whales in the 1984–88 Atlantic mackerel fishery despite fewer days on grounds than GDR vessels. These takes appear to be more related to differences in fishing strategies (i.e., gear configuration, trawling and haulback speeds) than total effort. Currently there is insufficient information to evaluate the effect of different fishing techniques between countries on the total take or the k/d rates. Increased observer coverage and documentation of fishing activities should be helpful in evaluating and developing recommendations for modifying current fishing practices, resulting in a reduction of incidental marine mammal mortality.

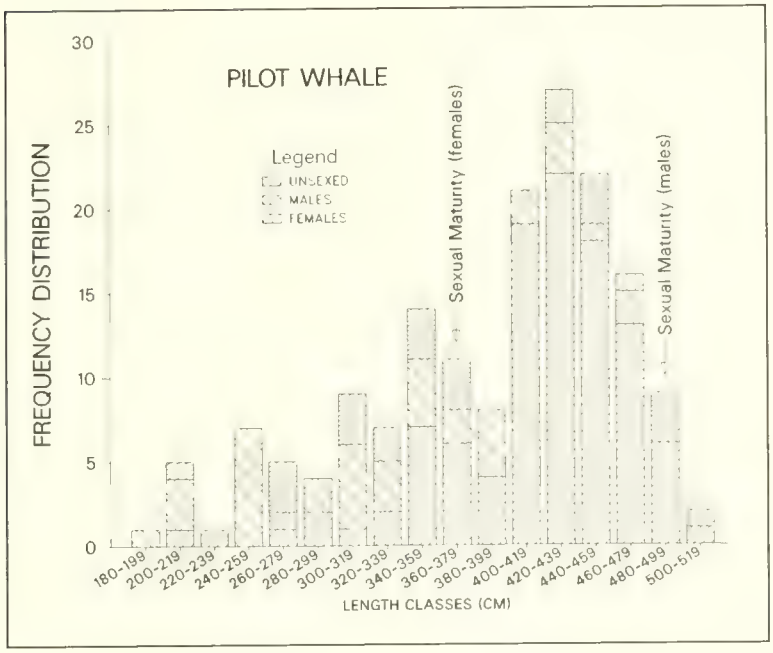

Figure 5
Length distribution of incidentally captured pilot whales measured by observers aboard foreign fishing vessels off the northeastern United States, 1986–88. Size at attainment of sexual maturity is from Perrin and Reilly (1984).

Incidental take of common dolphins and pilot whales relative to time of day and fishery

Significantly more common dolphins were captured during the *Loligo* fishery at night than during other time periods throughout the day. Possibly the diurnal movement upward at night would concentrate *Loligo* nearer the surface, thereby also concentrating common dolphins feeding on this prey. This would result in an increased likelihood of common dolphins capture due to a narrowing of the fishing area within the water column.

If common dolphins follow squids downward during daylight hours, then this would account for the lack of surface-feeding observations during the daytime. Conversely, if common dolphins feed principally at night, then common dolphins might become spatially separated from squid during daylight hours, resulting in a decreased likelihood of incidental capture. Although the reasons that common dolphins are caught at night in the DWF *Loligo* fishery are not readily apparent, it does seem that the day/night differences in capture are also related to a behavioral phenomenon of the dolphins, and not simply fishing practices.

Conversely, the take of pilot whales was significantly greater during daylight hours. Pilot whales were observed on numerous occasions in active pursuit and opportunistically feeding in and around the mouth of the net during haulback operations. Similar observations have been reported for the Pacific bottlenose dolphin and other species in Leatherwood (1975). The large size and widespread opening of pelagic mackerel trawls might serve to corral larger delphinid species such as pilot whales. Current data do not allow conclusive determination of whether the high incidence of pilot whale mortality during daylight hours is behavioral or the result of fishing practices by the Netherlands, GDR, and Poland.

Food habits

Common dolphins have been reported to feed on a wide variety of epipelagic and mesopelagic schooling finfishes and squids (Collett et al. 1981, Fiscus 1982, Fiscus and Niggol 1965, Fitch and Brownell 1968, Jones 1981, Nishiwaki 1972, Norris and Prescott 1961, Major 1986). Prey items collected from stomachs of common dolphins captured in the DWF indicate that *Loligo* and Atlantic mackerel are important prey items for dolphins during midwinter in the shelf waters of the mid-Atlantic.

Information on the dietary habits of pilot whales is limited, but they are considered teuthophagous, feeding principally on squid with fish as an alternative. Atlantic cod and Greenland turbot *Reinhardtius hippoglossoides*, which were taken off Newfoundland by overwintering pilot whales when squid were not available, are the only finfish prey items reported from the northwest Atlantic (Sergeant 1962, Mercer 1975).

We have not examined any stomachs of pilot whales taken in the DWF squid fisheries. However, it seems likely, based on qualitative examination of the relative abundance and co-occurrence of pilot whales and *Loligo* and known preferences for squid from the literature,

that *Loligo* is a principal prey item of pilot whales in the shelf waters of the mid-Atlantic during late winter and early spring. It also seems apparent that Atlantic mackerel could be considered an important prey of pilot whales in the mid-Atlantic. This conclusion is based on the observations of pilot whales feeding around and in the opening of the mackerel trawls, the occurrence of mackerel in the stomachs of two pilot whales taken in the Atlantic mackerel fishery, and the high incidence of mortality in the Atlantic mackerel fishery. It is possible, however, that feeding on Atlantic mackerel is an opportunistic phenomenon related to fisheries only, and that pilot whales do not otherwise prey significantly on mackerel.

Sex and maturity of common dolphins and pilot whales taken in foreign fishing operations

It is likely that most of the common dolphins killed in the *Loligo* and Atlantic mackerel fisheries were sexually immature. Estimates of total length at sexual maturity for male common dolphins are extremely variable between populations (Hui 1979, Perrin and Reilly 1984, Collett and Saint-Girons 1984). Collett and Saint-Girons (1984) found that, in the northeast Atlantic, sexual maturity in male common dolphins is reached at 200 cm, with animals <190 cm prepubescent. Several species of dolphins, including common dolphins, are known to travel in herds segregated by age and sex. In the northwest Atlantic, segregation by age and sex has been found in bottlenose dolphins (Irvine et al. 1981, Shane et al. 1986) and the harbor porpoise (Gaskin 1982). Irvine et al. (1981) found that subadult males formed bachelor groups, and sexually mature adult males rarely mixed with subadult males. Also, male and subadult female dolphins may follow fishing nets more often than females with calves. The dolphins reported in Table 6 were not captured simultaneously (i.e., having come from one group or pod) but rather were captured on several separate occasions. Although female common dolphins with calves have been observed in the areas of foreign fishing activity, none have been captured during trawling operations.

The size/sex composition of pilot whales killed in the Atlantic mackerel fishery indicates that most of the animals were sexually mature females. The size and sex ratios of pilot whales killed in the Atlantic mackerel fishery are similar to those ratios observed from pilot whale mass strandings in New England waters (Greg Early, New England Aquarium, Boston, MA, pers. commun., May 1988). Pilot whales are gregarious and social groupings are believed to be comprised of several sexually mature females and a few mature males (Martin et al. 1987).

Incidental take of common dolphins and pilot whales relative to available abundance estimates for each species

Estimates of the total number of common dolphins and pilot whales are available both for the shelf-edge alone and the combined all-shelf and shelf-edge waters of the northeastern United States (an area which is contained within the EEZ) by season (CETAP 1982). These estimates are based on standardized aerial surveys conducted during November 1978–January 1982, using line-transect methodology. Although these estimates are not for the same time period as the majority of the incidental take described in this paper, and these estimates have very high degrees of uncertainty (e.g., standard deviations of the estimates equal to the estimates themselves), they are the only population estimates available which can provide an indication of the relative magnitude of these incidental takes.

The shelf-edge abundance estimate for common dolphins during winter (most incidental takes for this species occurred during December and February) is 15,703 (CV 0.78) (CETAP 1982, table 17, p. 261). The average take per year for 1977–88 was 17 and 39 in 1984–88. These takes represent 0.11% and 0.25% of the winter abundance estimate. The maximum annual rate of take based on this winter abundance estimate was 0.48 ($n = 76$) in 1986 and was nearly twice the 1984–88 average.

Similar CETAP shelf-edge estimates for pilot whales during spring and summer are 6823 (CV 0.52) (spring) and 5251 (CV 079) (summer) (CETAP 1982, table 15, p. 233). The average take per year for 1977–88 was 25 and 46 in 1984–88. These takes represent 0.37% and 0.67% (spring) and 0.48% and 0.88% (summer) of the average seasonal abundance estimates for this species. The maximum annual rate of take based on the spring and summer abundance estimates, respectively, were 2.01% and 2.70% ($n = 142$) in 1988 and were three times the 1984–88 spring and summer rates of take.

The shelf-wide abundance estimates for common dolphins 31,124 (CV 0.59) (winter), and pilot whales 11,417 (CV 0.37) (spring) and 9808 (CV 0.66) (summer) are nearly twice the shelf-edge estimates, which reduces the above estimated rates of incidental take by nearly 50% if animals from the shelf-edge and shelf are considered as a single population.

To place pilot whale takes within the EEZ in perspective, present pilot whale incidental kill levels are comparable with recent mass strandings in New England waters (Greg Early, New England Aquarium, Boston, MA, pers. commun., May 1988). They do not approach the mortalities reported by Mercer (1975) for the historical Newfoundland drive fisheries (1948–71: Total 54,248; average 2260/yr). The impact of trophic

changes in the offshore cetacean communities, and the unknown DWF incidental mortality levels on components of the dolphin stocks when the DWF is fishing outside the EEZ, may be more of a factor in structuring present dolphin population trends than the levels of incidental takes that occur within the EEZ.

Also, we do not know the historical rates of take during the period 1960–76, when over 100 fishing vessels operated inside the EEZ per year. Since these fleets were not restricted by time or space, it is not unreasonable to assume that the number of dolphins taken pre-MFCMA were equal to or greater than the present. However, extrapolation of current levels of take to historical DWF fishing effort off the U.S. east coast (beyond speculation) would not be appropriate for several reasons. These include differences in the spatial/seasonal components of the fisheries over time and changes in the principal targeted species that have occurred during the past several decades. Likewise, the marine mammal/finfish/squid associations might have, likewise, changed during this time period. Also, technological changes in fishing gear and vessels have improved greatly during the past two decades, which might have increased the rate of take in recent years. Changes in the nationalities, and their associated fishing techniques, represented in the DWF have also occurred and could effect the rate of take of mammal species.

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Abstract.—A study was made of age, growth, and reproduction of the king mackerel *Scomberomorus cavalla* in Trinidad waters captured by hook-and-line and drift gillnets. Ages, estimated from otolith rings, ranged from 0 to VII in males and from 0 to X in females. Mean back-calculated lengths in 99 males ranged from 43.7 cm FL at the end of year I to 85.9 cm FL at the end of year VI, and in 233 females from 41.8 cm FL at the end of year I to 105.6 cm FL at the end of year VIII. The von Bertalanffy growth equations were for males, $L_\infty = 112.3\,[1 - \exp(-0.18(t + 1.80))]$ and for females $L_\infty = 140.1\,[1 - \exp(-0.15(t + 1.52))]$. Based on gonad examination of 97 males and 224 females, spawning takes place throughout the year around the island, with peak spawning from October through March, a period associated with low salinity. First spawning takes place at ages I–II for both sexes. Females predominated in all size groups, with the proportion of males increasing during the peak spawning season.

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Age, Growth, and Reproduction of the King Mackerel *Scomberomorus cavalla* (Cuvier) in Trinidad waters

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The king mackerel *Scomberomorus cavalla* (Cuvier) (Scombridae) occurs in coastal waters of the western Atlantic ranging from the Gulf of Maine to Rio de Janiero (Briggs 1958). It has also been reported throughout most of the West Indies (Erdman 1949), and its distribution is said to extend eastwards to Africa (Jordan et al. 1930). However, more recent reviews (Collette and Russo 1979) make no mention of *S. cavalla* in the Eastern Atlantic, although it has been reported from St. Paul's Rocks, a group of small islands in the mid-Atlantic (Lubbock and Edwards 1981).

Scomberomorus cavalla has commercial and recreational value throughout its range. Griffiths (1971) considered *Scomberomorus* spp., especially *S. cavalla* and *S. maculatus* (= *S. brasiliensis* Collette et al. 1978) to have greater commercial potential than the tunas in Venezuela. The general biology of *S. cavalla* has been investigated in North American waters (Beaumariage 1973) and off the state of Ceara, northeastern Brazil, including age and growth studies (Nomura and Rodrigues 1967, Ximenes et al. 1978). Manooch et al. (1978) provided a useful annotated bibliography on this species, and many aspects of its biology and fishery have been summarized by Collette and Russo (1984). More recent work includes studies on reproduction (Finucane et al. 1986) and growth (Manooch et al. 1987) in North American waters.

In Trinidad, Whiteleather and Brown (1945) and more recently Sturm et al. (1984) reported that *S. cavalla* approached *S. maculatus* (= *S. brasiliensis*) as the most abundant continental pelagic species in commercial landings. The *Scomberomorus* fishery in Trinidad is artisanal and seasonal from March through October, and *S. cavalla* is caught mainly by hook-and-line (trolling and live-bait fishing) and drift gillnets (Sturm et al. 1984). This paper provides information on age, growth, and reproduction of *S. cavalla* (the kingfish or thazard) in Trinidad waters.

Materials and methods

The climate of Trinidad is tropical, with a wet season from June to December. The surrounding waters are mainly estuarine. Surface temperatures vary little, ranging from 27 to 29°C (van Andel and Postma 1954, Edwards 1983). Further details of the study area may be found in Sturm (1978).

Fish were bought from artisanal fishermen in 1981–82 at six beaches: Maracas and Las Cuevas in the north, Mayaro and Guayaguayare in the southeast, and Cedros and Icacos in the southwest of the island. Artisanal catches consisted mainly of both *Scomberomorus* species, which on being landed were separated into baskets. There were usually not more than about a dozen boats fishing on any

one day from a beach, and catch per boat of *S. cavalla* was usually small (<20 fish). Not more than three catches were sampled up to a maximum of about 25 fish per sampling day, to enable accuracy of sample treatment in the field. Entire catches were sampled, and when this was not possible, large fish (>90 cm FL) and/or small fish (<50 cm FL), when present, were selected to direct attention to the ends of the distribution, and the rest of the sample was taken at random. A total of 363 fish was obtained, 190 from hook-and-line, 165 from gillnets (average stretched mesh size 113 mm), and eight from beach seines. In addition, 264 fish were measured at the Port of Spain Fish Market. Fish were measured to the nearest 0.5 cm fork length (FL) and weighed to the nearest 20 g. Gonads were weighed to the nearest 10 g.

Otoliths (sagittae) were used to age *S. cavalla*. When viewed in a black dish containing water in reflected light under a binocular microscope (×10), the otoliths revealed opaque and translucent rings. The non-marginal opaque rings were counted as annuli following Beaumariage (1973), Ximenes et al. (1978), Johnson et al. (1983), and Manooch et al. (1987), and distances were measured along the longitudinal axis from the focus to the distal edge of each opaque ring and to the edge of the otolith. One person read the otoliths.

The relationship between fork length and otolith radius was determined by regression analysis using both linear and quadratic models. When the relationship was established, fork length at age was back-calculated using methods of Bagenal and Tesch (1978).

The von Bertalanffy growth equation (1938)—$L_t = L_\infty\,[1 - \exp(-K(t + t_0))]$ where L_t = fork length at age t, L_∞ = asymptotic fork length, K = growth coefficient, and t_0 = time when length is theoretically zero—was fitted to weighted mean back-calculated lengths using an MS-DOS/BASIC version of a computer program by Sparre (1987).

Macroscopic stages of gonad development for both sexes were identified as described for *S. maculatus* (= *S. brasiliensis*) by Sturm (1978). They were immature-inactive, immature-developing, ripe, and ripe-running. The gonadosomatic index (GSI) was computed by dividing gonad weight by total fish weight and multiplying by 100.

Results

Size composition of material examined

Length frequencies of *Scomberomorus cavalla* samples from gillnets and hook-and-line were approximately similar. Hook-and-line apparently selected slightly larger fish—45–114.5 cm FL, with a modal length between 66 and 70 cm FL—than gillnets, which selected fish between 38.5 and 105 cm FL, with a modal length of between 61 and 65 cm FL (Fig. 1). The largest fish sampled was a 127-cm FL female caught in a beach seine. The size range of fish measured at the Port of Spain Fish Market was 37–135 cm FL with a modal length of 61–65 cm FL.

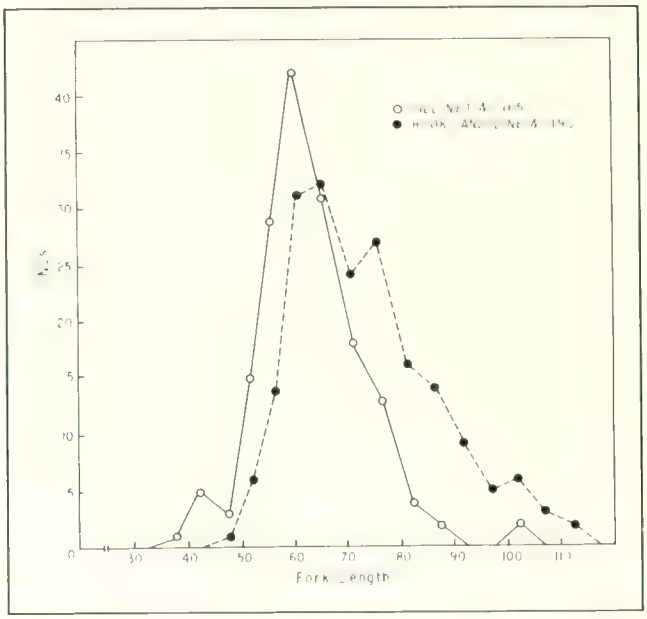

Figure 1
Length frequencies of gill net and hook-and-line samples of *Scomberomorus cavalla* from Trinidad waters. Lengths are grouped into 5-cm intervals. N = number of fish sampled.

Age and growth

Only 2 of 341 otoliths were considered illegible. However, not all of the remaining 339 otoliths had clear rings, though 85% were read with confidence. The main difficulty was determining the extent of the first opaque ring. The remaining 15% (52) were reread, with 79% (41) agreement between the two readings. The remaining 11 otoliths were then given new readings. For tracing the frequency of opaque-edged otoliths throughout the year, the data were grouped in bimonthly intervals due to the scarcity of data in non-seasonal months (Fig. 2). Otoliths with opaque edges were found throughout the year. The minimum percentage (20%) occurred in August–September after which there was a large increase to maximum percentages (60%, 58%, and 57%) from October through March, followed by 36% and 35% in April–May and June–July, respectively. These results suggest that opaque rings are formed

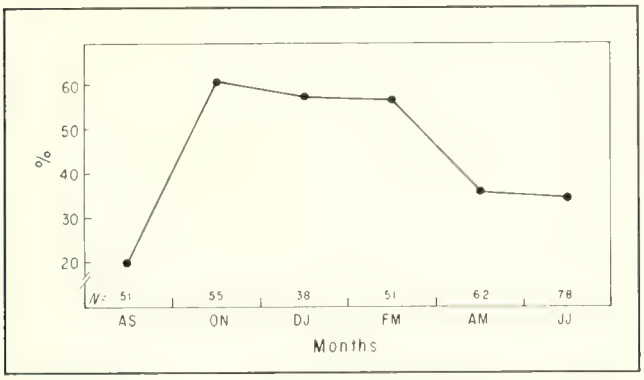

Figure 2
Bimonthly percentages of otoliths of *Scomberomorus cavalla* with opaque edges. N = number of fish sampled.

annually, mainly from October through March. Time of ring formation is similar to that recorded for Brazilian *S. cavalla* (Ximenes et al. 1978).

The relationship between fork length (FL) and otolith radius (OR) was represented by the following linear equations:

$$\text{Males: } FL = -1.73 + 1.49OR \ (r = 0.86)$$
$$\text{Females: } FL = -11.64 + 1.76OR \ (r = 0.90)$$

The intercepts were significantly different at the $P<0.001$ level ($F = 14.76$, df = 1, 336); therefore, the data were treated separately. Second-degree quadratic models were fitted to the separate data, but analysis of variance did not show significant curvature for males ($F = 3.03$, df = 1, 98, $P>0.05$) nor females ($F = 1.65$, df = 1, 235, $P>0.1$), therefore the linear equations were used to back-calculate length from age for males and females separately.

Observed and back-calculated lengths for 99 male and 233 female *S. cavalla* are shown in Table 1. Five age-0 fish (38.5–57.5 cm FL) were also recorded. The oldest male was age VII and the oldest female age X, but these were not included in the back-calculations. Length variation within age groups was large, as was the case for southeastern United States populations (Beaumariage 1973, Johnson et al. 1983). For example, age-II females ranged from 43.0 to 85.5 cm FL. From age II onwards, females grow faster than males. Figure 3 compares back-calculated growth of *S. cavalla* from Trinidad with that from southeastern United

Table 1
Mean observed and back-calculated lengths (cm) for *Scomberomorus cavalla* from Trinidad waters.

Age group	N	Mean observed length	Range	Mean back-calculated length at age							
				I	II	III	IV	V	VI	VII	VIII
Males											
I	23	57.3	44.0–72.5	44.9							
II	34	64.5	53.5–75.0	42.5	57.8						
III	25	71.4	62.5–78.0	44.6	58.4	66.9					
IV	9	72.2	65.5–81.0	41.5	54.5	61.8	68.3				
V	6	81.8	77.5–86.5	44.2	58.1	67.5	73.6	78.8			
VI	2	87.5	80.5–94.5	46.4	58.5	68.9	74.6	81.0	85.9		
Weighted mean				43.7	57.6	66.0	70.9	79.3	85.9		
N				99	76	42	17	8	2		
SD				5.0	5.3	5.2	5.5	4.3	9.8		
Annual increment					13.9	8.4	4.9	8.4	6.6		
Females											
I	46	58.2	42.0–70.5	43.7							
II	68	67.4	43.0–83.5	42.3	59.7						
III	48	71.8	62.0–93.5	39.8	57.1	66.7					
IV	33	80.2	65.0–101.0	41.1	57.6	67.4	75.1				
V	19	87.2	77.5–103.0	42.2	58.0	68.7	76.7	83.8			
VI	7	95.8	92.0–101.5	43.2	60.1	70.5	78.6	85.7	91.5		
VII	7	102.9	92.5–109.0	41.6	62.2	73.4	81.5	87.5	92.7	99.2	
VIII	5	109.7	101.0–127.0	39.9	59.8	70.0	79.6	88.4	95.8	101.2	105.6
Weighted mean				41.8	58.6	68.0	76.8	85.1	93.1	100.1	105.6
N				233	187	119	71	38	19	12	5
SD				5.7	6.2	7.0	6.8	6.2	5.4	1.9	9.9
Annual increment					16.8	9.4	8.8	8.3	8.7	7.0	5.5

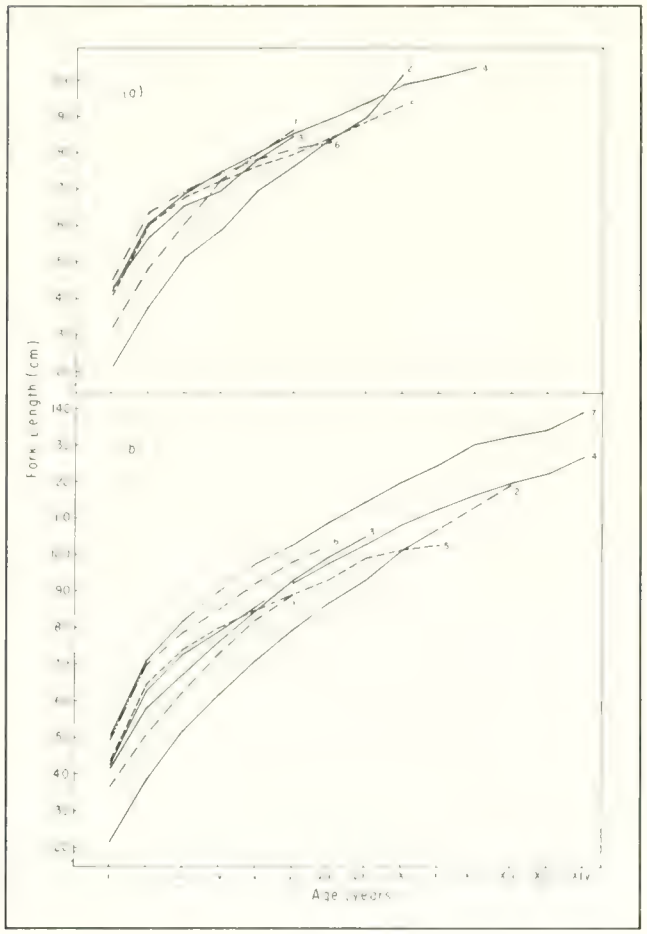

Figure 3

Growth (mean back-calculated fork lengths) of *Scomberomorus cavalla* (a) males and (b) females. 1 = Northeastern Brazil (Ximenes et al. 1978); 2 = Northeastern Brazil (Nomura and Rodrigues 1967), ages III and above observed lengths; 3 = Trinidad, this study; 4 = U.S. Gulf of Mexico (Manooch et al. 1987); 5 = Southeastern U.S., excl. La. (Johnson et al. 1983); 6 = Florida (Beaumariage 1973), fork length transformed from standard length by his formula FL = 1.096SL − 17.143; 7 = Southeastern U.S. incl. La. (Johnson et al. 1983).

States and northeastern Brazil. For both sexes, there is wide separation of lengths at age I, with those of Trinidad and North American fish being larger than those of Brazilian fish. The largest male lengths are from the Florida sample (Beaumariage 1973) up to age IV, and the smallest are for fish sampled in Brazil by Nomura and Rodrigues (1967) up to age VI. For females, the largest lengths are again for Beaumariage's sample except for an anomalous population of large females sampled in Louisiana (Johnson et al. 1983), and the smallest lengths are similarly for Nomura and Rodrigues' Brazilian sample. Back-calculated lengths at age of Trinidad fish lie between the larger lengths of North American fish and the smaller lengths of Brazilian fish, up to age III for males (82.8% of the sample) and age V for females (91.9% of the sample). The growth curve of Trinidad males closely resembles those from the southeastern United States presented by Johnson et al. (1983) and Manooch et al. (1987) up to age V, whereas the growth of Trinidad females is more similar to that of Brazilian females sampled by Ximenes et al. (1978). Growth rates of males from the different areas are similar up to age II, with Brazilian males showing less incremental decrease in the later ages. The same trend is shown for females, with marked incremental decrease being shown by southeastern United States (excluding Louisiana) females sampled by Johnson et al. (1983).

The von Bertalanffy growth parameters of Trinidad *S. cavalla* are presented in Table 2 along with those from southeastern United States and Brazil. Asymptotic lengths are larger for females than males. The asymptotic lengths of Trinidad and Brazil males are close, and much larger than those from North America, except for the recent study from the Gulf of Mexico (Manooch et al. 1987). For females, the pattern is somewhat similar, with the Trinidad and Gulf of Mexico values being the largest, except for the additional sample of large females from Louisiana (Johnson et al. 1983). For both sexes the K values are fairly close, the lowest coming from Trinidad, Brazil, and the Gulf of Mexico, with again the exception of the Louisiana females.

Size and age at first maturity

There were 14 ripe males (11 ripe + three ripe-running) and three ripe females in the age-I group, indicating first spawning for both sexes to take place in this age group. The shortest ripe male was 54.5 cm, and the largest immature developing male was 80 cm. The shortest ripe female was 58.5 cm, and the largest immature developing female was 114.5 cm. These sizes at maturity indicate that first spawning for both sexes may also take place at age II (Table 1).

Gonad analysis and GSI

Gonad stages and corresponding GSI values are shown in Table 3. No ripe-running females nor spent fish were observed in this study. Figures 4 and 5 show gonad analysis of the 97 males and 224 females that were capable of spawning as indicated by size at first maturity. Of these, 70 males and 164 females were analyzed for GSI, and the results are also shown in Figures 4 and 5. Male gonad analysis was more difficult because milt was present in the early stages of gonad development; this explained the trend to higher percentages of ripe males. Ripe fish were present during all months

Table 2

von Bertalanffy growth parameters for *Scomberomorus cavalla* from Trinidad, southeastern United States, and Brazil.

Area and source	L_∞ (FL cm)	K	t_o (yr)
Males			
Trinidad (this study)	112.3	0.180	−1.79
Northeastern Brazil (Nomura and Rodrigues 1967)	116.0	0.180	−0.22
Northeastern Brazil (Ximenes et al. 1978)	113.3	0.229	−1.50*
Florida (Beaumariage 1973)	90.3**	0.350	−2.50
Southeastern U.S. (Johnson et al. 1983)	96.5	0.280	−1.17
U.S. Gulf of Mexico (Manooch et al. 1987)	111.3	0.208	−1.48
Females			
Trinidad (this study)	140.1	0.150	−1.52
Northeastern Brazil (Nomura and Rodrigues 1967)	137.0	0.150	−0.13
Northeastern Brazil (Ximenes et al. 1978)	131.7	0.164	−2.00*
Florida (Beaumariage 1973)	124.3**	0.210	−2.40
Southestern U.S., excl. La. (Johnson et al. 1983)	106.7	0.290	−0.97
Southeastern U.S., La. (Johnson et al. 1983)	152.9	0.140	−2.08
U.S. Gulf of Mexico (Manooch et al. 1987)	141.7	0.136	−1.98

*Assumed negative.
**Calculated from Beaumariage's formula FL = 1.096SL − 17.143.

Table 3

Gonad stages and gonadosomatic indices of *Scomberomorus cavalla* from Trinidad waters.

	Males			Females		
Gonad stage	*N*	Mean GSI	Range GSI	*N*	Mean GSI	Range GSI
Immature inactive	2	0.77	0.32–1.37	10	0.58	0.41–1.16
Immature developing	21	0.38	0.14–0.78	113	0.63	0.16–1.37
Ripe	18	0.92	0.30–1.92	41	1.75	0.41–5.68
Ripe running	29	1.11	0.33–3.73	—	—	—

except December (when only nine fish were sampled), and ripe females were absent in April. Maximum percentages of females occurred from September to October and January to March. GSIs for females peaked in September, November, January, and February. Males showed similar patterns, though data were more limited. The above observations indicated that *S. cavalla* spawns throughout the year with more intense spawning from September through March.

Sex ratio

Females were dominant in all size groups, both in gillnet and hook-and-line samples, and in the peak spawning and non-peak spawning seasons (Table 4). The degree of dominance varied with size class, type of gear, and season. Dominance increased with size class, and all but a single specimen over 90 cm FL was female. Females predominated to a greater extent in the hook-and-line samples compared with gillnet samples. In gillnet samples, the proportion of females decreased from 74% during the non-peak spawning season to 62% during the peak spawning season, which corresponded with an overall decrease in females from 77% to 63% in the respective seasons. In the southeastern United States, the sex ratio was also found to favor females (Fischer 1980, Trent et al. 1983).

Discussion

Evidence for time of annulus formation in Trinidad *Scomberomorus cavalla* is weak. Tracing of otolith edges throughout the year suffered from a paucity of

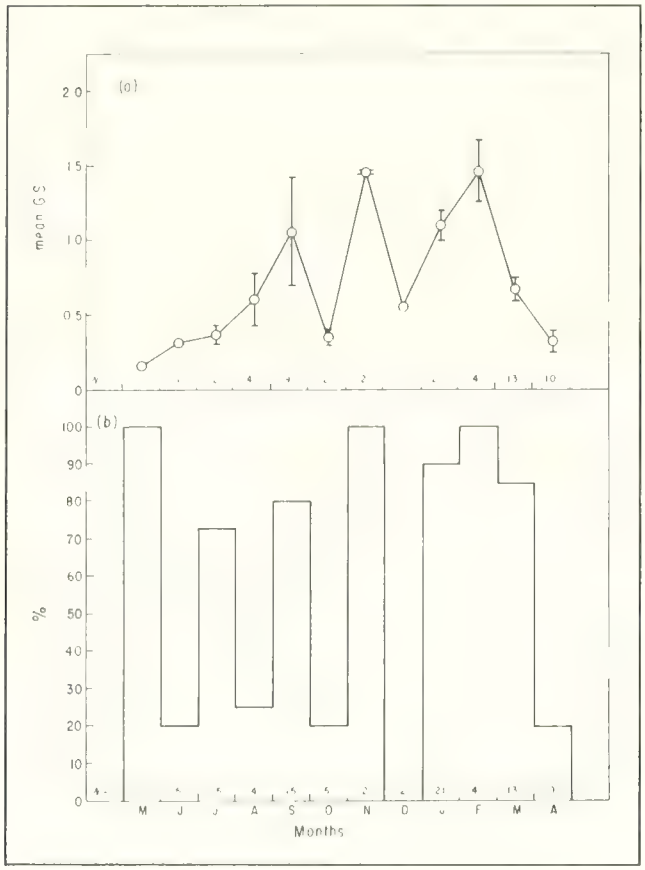

Figure 4
Seasonal maturation cycle of male *Scomberomorus cavalla* (>54.5 cm) by (a) mean monthly GSI and (b) monthly percentages of ripe (ripe and ripe-running) gonads. N = number of fish sampled.

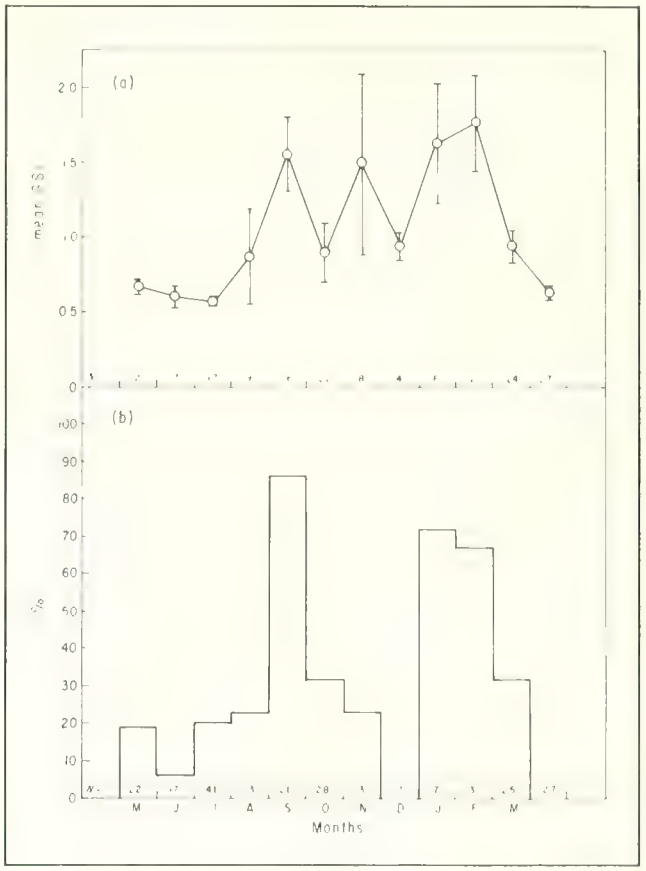

Figure 5
Seasonal maturation cycle of female *Scomberomorus cavalla* (>58.5 cm) by (a) mean monthly GSI and (b) monthly percentages of ripe gonads. N = number of fish sampled.

data when the annulus is apparently formed as fish were scarce from November to February. Maximum (bimonthly) percentages of opaque otolith margins compare well with those (monthly) of North American studies (Beaumariage 1973, Johnson et al. 1983, Manooch et al. 1987). However, in the present study the minimum (bimonthly) percentage (20%) was much higher than in North America where in all the studies there were one or more months with no edged otoliths. In Trinidad the period September to March, when maximum percentages of opaque otolith margins are found, corresponds with the period of greatest spawning intensity. In Brazil, the opaque ring is laid down from November to March corresponding to a period of intense spawning (Ximenes et al. 1978). Otoliths of North American fish generally had the largest percentages of opaque margins from April through June (Beaumariage 1973, Johnson et al. 1983, Manooch et al. 1987) at the start of a well-defined spawning season (Beaumariage 1973, Finucane et al. 1986). The process of spawning may therefore be related to annulus formation in *S. cavalla*. If first spawning takes place at age II, as might occur on occasion for Trinidad *S. cavalla*, an annulus in immature (age-I) fish may be explained by some internal physiological rhythm, together with the environmental changes that trigger spawning, causing annulus formation. This explanation was put forward for annulus formation in immature fish for hake *Merluccius merluccius* (Hickling 1935) and red snapper *Lutjanus campechanus* (Nelson and Manooch 1982). As spawning is year-round in the tropical waters around Trinidad, the finding of relatively large numbers of opaque margined otoliths in the months outside the period of their maximum occurrence during peak spawning can be expected. These, however, obscure the results of tracing the frequency of otolith edges throughout the year compared with the more clear-cut results from the more temperate North American waters.

The differences in length at age and theoretical growth parameters between Trinidad, Brazilian, and North American fish may result from different environ-

Table 4
Sex ratio of *Scomberomorus cavalla* from Trinidad waters.

Length range (cm)	Gillnets			Hook-and-line			Totals		
	Male	Female		Male	Female		Male	Female	
	(*N*)	(*N*)	(%)	(*N*)	(*N*)	(%)	(*N*)	(*N*)	(%)
Peak spawning (September–March)									
30.0–49.5	1	0	0	0	1	100			
50.0–69.5	24	36	60	10	24	71			
70.0–89.5	18	12	40	9	29	76			
90.0–109.5	0	1	—	1	11	92			
110.0–130.5	0	0	—	0	0	—			
Total	43	49	53	20	65	76	63	114	60
Non-peak spawning (April–August)									
30.0–49.5	1	6	86	0	0	—			
50.0–69.5	14	39	74	14	26	65			
70.0–89.5	4	7	64	8	42	84			
90.0–109.5	0	2	100	0	13	100			
110.0–130.5	0	0	—	0	2	100			
Total	19	54	74	22	83	79	41	137	77
Totals	62	103	62	42	148	78			

ments, feeding habits, exploitation rates, methods of capture, sample sizes, etc. The fishery in North America is better developed than in Brazil (Collette and Russo 1984) and Trinidad, which enabled larger samples for age and growth studies to be collected from the former region. There were considerable differences between sample sizes of older fish in the various studies, which could introduce bias in the comparison of von Bertalanffy parameters. Best representation of growth of older fish came from Manooch et al. (1987) and the anomalous group of Louisiana females (Johnson et al. 1983). Changes in populations between studies brought about by exploitation and other factors could also influence the results.

Different methodologies could also contribute to these differences. Nomura and Rodrigues (1967) counted translucent rings to age Brazilian fish, thus omitting part of a year. This probably resulted in their obtaining the slowest growth of all the studies. Back-calculated lengths were fitted to the von Bertalanffy equation by Ximenes et al. (1978), Johnson et al. (1983), and in this report. Beaumariage (1973) fitted observed standard lengths and advised caution in extrapolation of the theoretical growth curve for size at older ages, because it was derived from Walford plots that excluded older fish; this resulted in conservative estimates. Nomura and Rodrigues (1967) used both back-calculated and observed lengths, which probably resulted in large values of L_∞. Other differences in methodology, e.g., the weighting of mean back-calculated and observed lengths and more exact fitting of the von Bertalanffy curve using computer programs in the later studies, and the non-use of an intercept value for back-calculation in some of the studies, could lead to minor differences in the results. Comparisons of results between the three areas evidently cannot be properly done due to differing sample sizes and methodologies.

Estimates of maturity of 58.5 cm FL or age I–II for Trinidad female *S. cavalla* generally agree well with those of other studies. In Brazil, first maturity was found to take place at 58.6 cm FL (Alves and Tome 1967) and 63.5 cm FL or age III (Gesteria and Mesquita 1976). Another study showed that females first matured between 43.5 and 56.5 cm FL or age III, with 50% maturity at 77 cm FL or age V–VI (Ivo 1972). Size of maturity of Trinidad females compares well with that in Brazil. However, greater age at maturity of Brazilian fish could be due to overestimated age at length based on the use of translucent rings for ageing by Nomura and Rodrigues (1967). Finucane et al. (1986) reported size at maturity at 44.9 cm FL in the southeastern United States. In Florida waters, Beaumariage (1973) round ripe eggs in age-I females (61.4 cm SL = 65.6 cm FL) similar to Trinidad results. However, he concluded that these eggs were aborted or reabsorbed, and spawning did not really take place until age IV (88.0 cm FL). As with females, ripe males

first appeared at age I (63.4 cm FL) as they did in Trinidad, but Beaumariage believed that males spawned initially at age III (77.0 cm FL) due to the greater development of spermatogenesis in the testes of older fish. However, in Trinidad initial spawning takes place at age I, as shown by the presence of ripe-running males in this age group.

The spawning pattern of *S. cavalla* in Trinidad is apparently similar to that off the coast of Ceara, in northeastern Brazil. Gesteria and Mesquita (1976) observed year-round spawning with maximum intensity from October through March, as in Trinidad. Spawning throughout the year was also recorded by Ivo (1972), but his period of maximum activity was from January through June. Another study (Menezes 1969) indicated that they spawn during the period October through March. Further north, the spawning season is reversed, where in the northeastern Caribbean it lasts from April through November (Erdman 1976) and in the southeastern United States, from April through October (Beaumariage 1973, Finucane et al. 1986). Spawning migrations in North America are determined by temperature (Moe 1972, Beaumariage 1973). In Trinidad, however, spawning and migration may be influenced by salinity changes because there is little variation in the water temperature. Peak spawning starts after the rains have set in, and may be triggered by a drop in salinity; minimum salinities have been recorded in August and September (van Andel and Postma 1954, Edwards 1983). The presence of ripe-running males in the samples indicates spawning in local waters, but the spawning grounds remain to be discovered. The scarcity of the fish during November through February remains unexplained. Spawning on the outer Continental Shelf, 50–60 km offshore, as occurs in the northwestern Gulf of Mexico (McEachran et al. 1980) would place part of the population beyond the reach of the artisanal fishing fleet which is limited to some 40 km offshore. Another possible factor could be migration along the Venezuelan coast to the northwest and/or the southeast, although part of the population may be resident throughout the year. Decreased vulnerability to hook-and-line due to decreased feeding activity during spawning, and/or gillnets due to spawning in waters deeper than that in which the gillnet is effective, are other possible reasons to be considered.

Beach landing data indicate that a southerly migration takes place in Trinidad during the months when the fish is seasonally abundant (Sturm et al. 1984). In the present study, gonad analysis did not suggest any migratory trends since ripe fish were taken around the coast throughout the year. Moreover, observations on stomach contents showed no clear feeding patterns as evidence of migration (unpubl. data). The spawning and abundance patterns of *S. cavalla* approximately correspond to those of *S. maculatus* (= *S. brasiliensis*), which spawns throughout the year with more intense spawning from October through April and is seasonally abundant from May through September (Sturm 1978). *S. brasiliensis* also moves in a southerly direction during peak abundance, part of likely clockwise movements around the island (Sturm 1978, Sturm et al. 1984). In Florida, Williams and Sutherland (1979) and Sutherland and Fable (1980) have shown that *S. cavalla* undertakes long-range migrations compared with the shorter range migrations of *S. maculatus*, which is closely related to *S. brasiliensis* (Collette et al. 1978). In Trinidad, a similar situation would explain the difficulty in recognizing migratory trends of *S. cavalla*, compared with the more local movements described for *S. brasiliensis* (Sturm 1978).

Female dominance in samples may be the result of more females than males being hatched or mortality being higher in males than females. Higher mortality probably is associated with slower growth in males. Alternatively, female dominance may be a function of gear selection in gillnets or of behavioral differences between the sexes. Increased voracity in females was recorded in Brazil (Menezes 1969) and may explain why the sex ratio favored females in hook-and-line samples. Also, males may inhabit greater depths than females and are less vulnerable to gillnets. If this was the case, a meeting of the sexes for spawning by an upward migration of males and/or a downward migration of females could explain the increase in the male:female ratio observed for gillnets during peak spawning.

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Leopard Shark *Triakis semifasciata* Distribution, Mortality Rate, Yield, and Stock Replenishment Estimates Based on a Tagging Study in San Francisco Bay

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Abstract.—Leopard shark tag recovery data, obtained from a 1979–88 study in San Francisco Bay, were analyzed to determine temporal and geographic distribution of the tagged population. Virtual population analysis of the tag recovery data was used to derive fishing mortality rates, which in turn were used to obtain yield-per-recruit and stock replacement values, and to estimate the effect of management by size limit on stock replenishment and yield per recruit.

Of the tagged population, 11% was recovered by sport anglers and commercial fishermen, and the distribution of recoveries indicates that leopard sharks are mostly resident in San Francisco Bay, although a portion of the population moves out of the Bay during fall and winter. An unusually high number of recaptures was made in 1983, a year of El Niño conditions and high river run-off. After obtaining mortality, yield, and stock replacement values, it was proposed that a viable management strategy for the San Francisco Bay leopard shark would be a size limit of 100 cm or 40 inches to ensure maintenance of the stock and provide a yield per recruit not too far below a maximum.

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Shark has now become a familiar item at seafood counters and on restaurant menus in the United States (Slosser 1987), while in the past these fish were often discarded as trash fish, or at best valued for fish meal or their vitamin A-rich livers (Frey 1971). California has seen the rise of four new commercial elasmobranch fisheries since the mid-1970s (Holts 1988), and recreational shark fishing has grown in popularity in California and in other coastal states (Ristori 1987). The relatively rapid increase in shark harvesting has created a pressing need for more biological information to support management of targeted species, particularly information relating to population structure, mortality and replenishment rates, and degree of exchange between stocks. Elasmobranchs may be particularly vulnerable to exploitation, because they are generally slow growing and produce relatively few young, with recruitment appearing to be largely determined by parental stock size (Holden 1977).

The leopard shark *Triakis semifasciata* is harvested both commercially and recreationally in California. It occurs along the coast from Baja California, Mexico, to Oregon, and is very common in northern California bays (Squire and Smith 1977, Eschmeyer et al. 1983). Its fairly large size (maximum recorded is 180 cm; Kato et al. 1967) and accessibility in nearshore areas and bays probably contribute to its appeal with anglers and small-scale commercial boat operators. Reported commercial landings in California since 1980 have ranged from 18,199 kg (40,085 lbs) in 1980 to 45,994 kg (101,309 lbs) landed in 1983 (Table 1), with the San Francisco area contributing a large portion of the catch. Recreational landings are comparatively larger, judging from estimates of landings compiled by the U.S. Department of Commerce Pacific Coast Marine Recreational Fishery Statistics Survey (Table 2). Recorded commercial landings of leopard sharks may be misleading, as leopard sharks are often lumped with other species under the general category "shark, unspecified." Because of this reporting bias, it is difficult to determine the full extent of the commercial harvest. Further, it should be noted that reliable data for stratifica-

Table 1

Reported commercial leopard shark landings (in kilos) by California port area. Source: Joyce Underhill, Calif. Dep. Fish Game, Long Beach, CA 90801, pers. commun., 17 May 1989.

Year	Eureka	San Francisco	Monterey	Santa Barbara	Los Angeles	San Diego	California total
1980	–	11 006	54	3 103	3 672	363	18 199
1981	94	12 334	55	5 505	3 482	1 913	23 384
1982	–	13 308	128	11 262	5 894	1 464	32 057
1983	–	33 764	202	7 218	2 632	2 177	45 994
1984	–	14 664	1 322	7 482	5 185	2 153	30 806
1985	24	8 054	7 620	8 135	8 725	1 871	34 430
1986	400	11 435	3 553	7 805	7 499	3 239	33 932
1987	741	6 684	3 523	6 357	6 113	1 720	25 138
1988*	1 263	2 367	2 038	5 161	3 728	4 357	18 914

*Preliminary.

Table 2

Reported commercial landings and estimates of the total marine recreational landings of leopard sharks in northern California, 1980–87. Recreational landings are Type A catches (observed landings) for north of San Luis Obispo County to the Oregon border, based on the Pacific Coast Marine Recreational Fishery Statistics Survey (provided by John F. Witzig, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv., Silver Spring, MD 20910, 14 June 1989). Commercial landings are summed for northern California ports.

	Northern California landings	
	Commercial	Recreational
Year	(kilos)	
1980	11 060	68 682
1981	12 484	62 664
1982	13 436	7 578
1983	33 966	116 517
1984	15 986	33 610
1985	15 698	131 787
1986	15 388	158 778
1987	10 948	289 097

tion of catch and effort by moderately small time or area segments are unavailable for either the recreational or commercial fisheries. The smallest divisions for the recreational fishery are northern and southern California. For the commercial fishery, only the place of landing and not the place of catch is recorded, and effort data are nonexistent.

Information on reproduction, stock replacement rates, and stock interaction is scanty and mostly undocumented. Estimates of length at maturity for males have ranged from 70 to 119 cm and for females from 100 to 129 cm; size at birth is about 20 cm (Ackerman 1971, Compagno 1984, Kusher 1987). The gestation period is estimated at 10–12 months and parturition takes place in spring, according to Ackerman (1971) who worked with Elkhorn Slough fish in Monterey County, California. Certain other observations corroborate this. Moser and Sakanari* examined an aggregate of pooled embryos from fish taken in the fall in San Francisco Bay and the measurements formed a unimodal distribution with little variation in embryo sizes among litters, which is the expected pattern for an annual reproductive cycle. More than one mode among litters would be observed for a gestation period of 2 or more years. In addition, R. Russo (East Bay Park Dist., Alameda, CA 94169, pers. commun., 27 March 1984), sampling in South San Francisco Bay, has noted a predominance of pregnant females with near-term pups mainly from March through June (April–May peak), indicating a once-a-year parturition in spring. Pupping could be annual and occur in alternate years, with a 'recuperative' year between, but then about half of the mature female population would be in a nonreproductive condition at any given time. Of the 90 females over 120 cm that Ackerman (1971) examined from Elkhorn Slough, 94% had embryos or fertilized eggs in at least one ovisac; and all females >110 cm total length (TL) collected by Kusher (1987) in Elkhorn Slough and Monterey Bay and San Francisco Bay showed signs of either pregnancy, recent birth, or embryo abortion. Therefore, we use the assumption of an annual reproductive cycle in later sections dealing with stock replacement by reproduction. The leopard shark is primarily a benthic feeder (Russo 1975, Talent

*Drs. M. Moser and J. Sakanari (Long Marine Lab., Univ. Calif., Santa Cruz, pers. commun., Sept. 1984) report that in a sample of nine pregnant females taken on 10 September 1984, presumably in midterm, the mean embryo length was 11.26 cm (1.51 SD), (n = 51 embryos).

1976). Prior to the work described here, nothing was known of its movements or the degree of exchange with other leopard shark populations along the California coast.

In 1979, a tagging study was initiated in San Francisco Bay to obtain information on age validation, growth, and movements of this species. Tag recaptures were monitored over a 9-year period. This report gives results of movements that were deduced from the temporal and geographic distribution of tag recoveries. In addition, although beyond the planned design of this study, we decided to utilize the tag recovery data together with published information to estimate the effect of management by size limit on stock replenishment and on yield per recruit. The lack of suitable statistical information on catches, as mentioned previously, prevented us from performing analyses that involve weighting tag recoveries by catch or effort. Results of the age validation segment of the study have been published elsewhere (Smith 1984), and results on age and growth are also being published separately (Kusher et al. In prep.).

Methods

All sharks were tagged off Hunters Point in south San Francisco Bay in 1979. Collections were made with a 183-m longline rigged with an average of 150 baited hooks fished on the bottom at depths of 15–20 m. Prior to release, total and precaudal lengths were recorded to the nearest centimeter, and each fish was given an intraperitoneal injection of oxytetracycline hydrochloride to mark vertebral centra for age verification purposes (Smith 1984). A record was made of the sex and general physical condition of each fish; seriously injured animals were not tagged. Those with minor hook injuries or with partially everted stomachs were classified as "injured"; the rest were classified as "healthy." A plastic rototag of the type recommended by Kato and Carvallo (1967) was applied to the first dorsal fin and the fish released at the capture point. The fin tags were imprinted with a legend informing the recoverer that a reward (amount unspecified) was offered for return of the tag and the fish or a section of its vertebral column for age verification purposes. The legend also provided an address and phone number to contact to arrange delivery.

Mortality estimation

Fishing mortality rates were estimated from the tagging data using the concept described by Murphy (1965), Gulland (1965), and Tomlinson (1970), which is now commonly referred to as virtual population analysis (VPA), though it differs from the original VPA procedure of Fry (1949). The computer program COHORT, written by John Geibel and Phil Law (Calif. Dep. Fish Game, 411 Burgess Drive, Menlo Park, CA 94025) was used to calculate the estimates. The natural mortality estimate was based on Hoenig's (1983) regression equation $\log (Z) = 1.46 - 1.01 \log (t_{max})$ where Z is the instantaneous annual total mortality coefficient and t_{max} is maximum age attained by the species. If the maximum age was determined from a period when there was virtually no fishing directed at the species, then one could assume the estimated Z approximates the instantaneous annual natural mortality coefficient, M.

The basic procedure involved assuming values of M over each 1-year time interval, taking a trial value of F_n, the instantaneous annual fishing mortality coefficient, for the ultimate interval, and executing the backward VPA computation on the tag recoveries to obtain an estimate of N_0, the number of tagged fish at the beginning of the first interval. Trial values were then iterated until the series converged on N_0.

Before conducting the VPA, it was necessary to consider two additional factors which would cause adjustments to the actual observations used in the analysis: (1) the likely rate of tag loss and (2) the level of tag recovery nonreporting. Since the tagging experiment was not designed for this type of analysis, there were no built-in procedures to estimate these factors. We therefore used what we judged to be the best available information from outside sources.

Yield per recruit

Yield per recruit was calculated by piecewise integration of the yield curve. The yield in weight at each age was taken to be the product of the annual rate of exploitation, the midpoint between an individual's weights at the beginning and end of the age interval, and the population size at the beginning of the interval.

$$Y = \exp[-M(t_{r'} + 1)]\,[1 - \exp(-Z)]\,(F/Z) \times \sum_{t \geq t_{r'}}^{t_{max}} \{\exp[-Z(t - t_{r'})]\}\bar{w}_t \qquad (1)$$

where Y is yield per recruit in weight (kg), t is age, $t_{r'}$ is age at first capture, and $\bar{w}_t$ is the midpoint between the weights at t and $t + 1$.

Weight at age was computed by using predicted values from the von Bertalanffy length equation from Kusher (1987) and the weight-length formula in Smith (1984). Note that equation (1) assumes constant M and Z except that natural mortality is doubled during

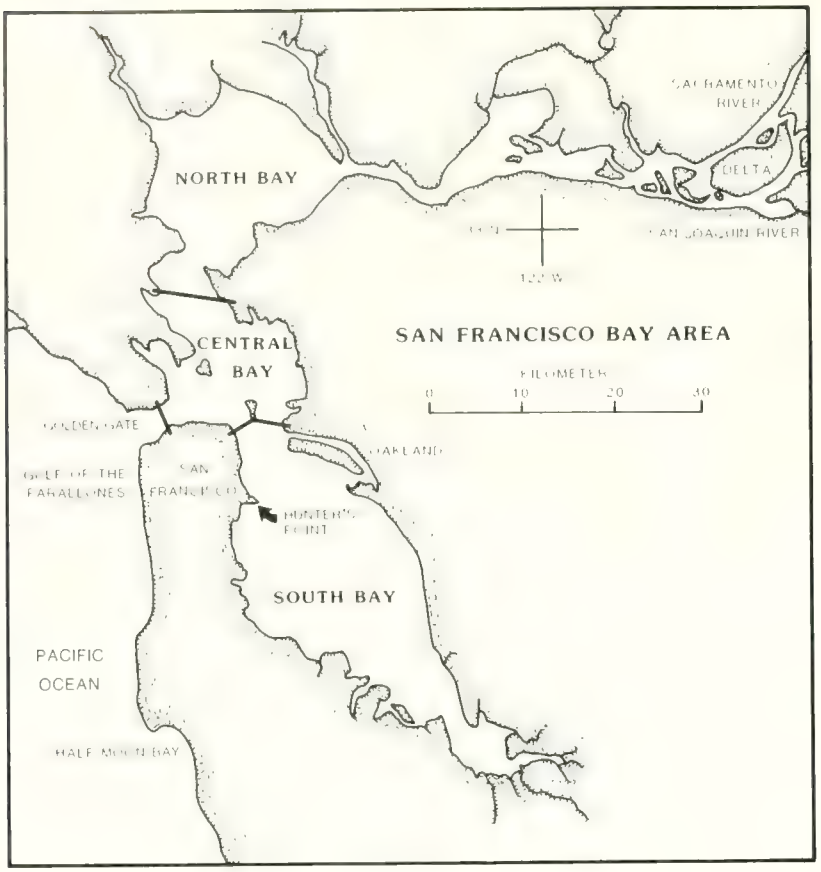

Figure 1
Map of San Francisco Bay showing location of release area (arrow) and major Bay Area divisions and names referred to in the text.

year 1. This gives some weight to a higher mortality these young fish must suffer relative to the adult sharks. The phenomenon of the young being preyed on by larger sharks has been cited by Springer (1960, 1967) and by Holden (1974).

Stock replacement

Also calculated for various levels of age at first capture (knife-edge selection) and fishing mortality were the percentages of stock which would be replaced due to reproduction. Assuming an even division among the sexes, this was done by summing over ages, from age at first maturity to maximum age, the products of the number of female survivors per recruit and the number of pups produced by females at each age above the age of maturity and multiplying this sum by 100. For given t_r, and F

$$R = \sum_{t \geq t_m} 50 \exp[-M(t+1) - F(t - t_r)\,\delta]\, P_t \qquad (2)$$

where t_m is female age at maturity, R is stock replacement per recruit in percent, P_t is estimated number of progeny produced annually by an age t female, and

$$\delta = \begin{cases} 1 & t > t_r \\ 0 & t \leq t_r \end{cases} \qquad (3)$$

Fecundity as a function of maternal body weight was estimated by fitting a monomolecular curve of the form $P_t = \beta - \theta\rho^{w(t)}$, with P the number of progeny, $w(t)$ the weight of the female at age t, and β, θ, and ρ constants. For computation, age at maturity was taken as the age corresponding to the weight which produced a value of zero for P_t in the above equation.

Ackerman (1971, his table 6) gives the numbers of embryos observed in 66 female leopard sharks ranging in size from 9.3 to 16.3 kg. Although his data are in a form which allows only the computation of mean number of embryos per female for five weight classes, he does give the number of females observed in each weight category. Using the numbers of females as weighting factors, the curve was fitted to these means with the Levenberg-Marquardt algorithm as implemented in the NCSS nonlinear regression program*.

*Number Cruncher Statistical System, Version 5.3–Power Pack, 1988. NCSS, Kaysville, UT 84037. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Progeny as a function of maternal age was then estimated by applying the weight-length-age relationships cited above. We assume all nondeformed embryos survive to time of birth. Data were not available for applying the preferable procedure of directly regressing fecundity on age.

Geographical names and location of the tagged-fish release area are given in Figure 1.

Results

Tagging

A total of 948 sharks were tagged off Hunters Point, San Francisco, in south San Francisco Bay between 26 July and 13 September 1979. Most were tagged in August (68%) and September (26%). The hook rate was very high: 22 *Triakis* per 100 hooks, and a 44% hook rate for all elasmobranchs. Other sharks and rays taken in order of abundance were brown smoothhound *Mustelus henlei* ($n = 872$), bat ray *Myliobatis californica* ($n = 159$), soupfin shark *Galeorhinus galeus* ($n = 6$), sevengill shark *Notorhynchus cepedianus* ($n = 5$), and spiny dogfish *Squalus acanthias* ($n = 2$).

The lengths of tagged leopard sharks ranged from 51 to 144 cm TL (mean 81 cm, Fig. 2). The male:female ratio was 53:47. Large individuals may have been underrepresented in the tagging, since only 9% of females and 11% of males were over 100 cm. Commercial fishermen have reported a higher proportion of large fish in their catches, fishing at the same time with similar gear but in different areas of the south bay (B. Van Gorp and B. Fraser, commercial shark fishermen, pers. commun., June 1980). On the other hand, leopard sharks were probably recruited to our gear at a larger size than would be true for typical sportfishing tackle. Anglers fishing from shore and piers using small hooks would surely take a higher percentage of fish under 70 cm than that shown in Figure 2.

Of the 948 fish tagged, 82 individuals were classified as "injured" and the remaining 866 fish as "healthy." Return rates would presumably be higher for healthy, uninjured fish than for injured fish if the tagging operation caused mortalities; the absence of such a difference could be taken as suggestive of little or no tagging-induced mortality (Gulland 1983).

Recoveries

As of 30 September 1988, 108 fish had been recaptured of which 101 had known recapture date and location. A breakdown of all methods of recapture is given in Table 3, and provides an interesting glimpse of the various users of the leopard shark resource. The proportions reported by each group should approximate the proportions of the natural population harvested or caught by each group.

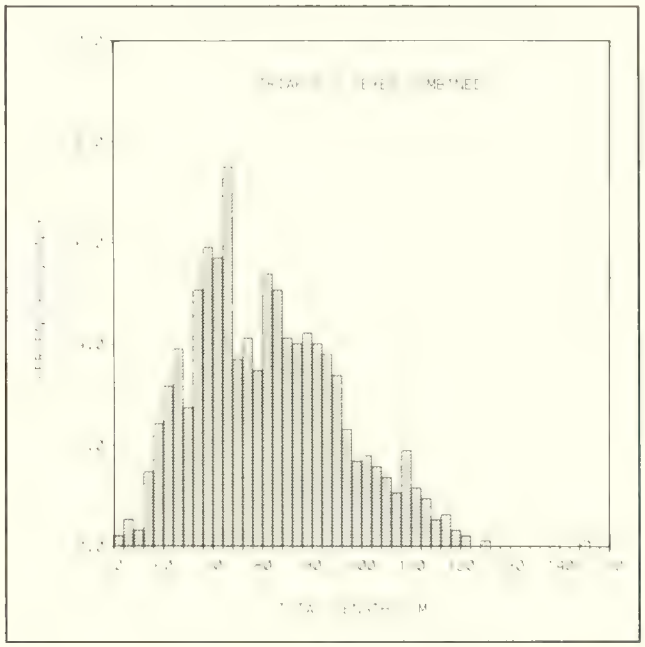

Figure 2
Length frequency of tagged leopard sharks (sexes combined) released off Hunter's Point in south San Francisco Bay, California, 1979.

Table 3
Distribution of leopard shark tag recaptures by recovery method and area in and around San Francisco Bay, California, 1979–88.

Method of recapture	Area of recapture: South bay	Central & north bays	Outside bay/ ocean	Totals
Recreational				
Private boat/skiff	32	15	1	48
Sportfishing boat (commercially operated)	0	4	0	4
Bank	13	3	2	18
Pier	10	6	0	16
Jetty	0	1	0	1
Bridge	1	0	0	1
Total	56	29	3	88
Commercial				
Bottom trawl	0	0	5	5
Gillnet	0	0	4	4
Longline	4	0	0	4
Total	4	0	9	13
Total all methods	60	29	12	101

Figure 3

Bimonthly distribution of leopard shark recoveries in and around San Francisco Bay, California, 1979–88, for which recapture location and date were known.

Of the recoveries, 81.5% were reported by sport anglers, 12.0% by commercial fishermen, and 6.5% of the fish were found on shore or had an unknown recapture method. Those recovered by recreational anglers were rather evenly divided between shore and boat anglers, with skiff fishermen dominating the latter category. The important role of recreational anglers in the recovery of tagged fish appears to reemphasize the predominance of recreational users of the leopard shark resource.

Over the 9-year period, most fish were recaptured during the months of September (20%) and June (13%);

the fewest were returned in February (2%), January (4%), and July (5%). The return rate for 'healthy' fish was 9.9% and that of 'injured' fish, 15.8%. Clearly, there is no indication that handling during the tagging process induced excess tagging mortality. The sex ratio of recaptured fish was exactly the same as at tagging (53% males) indicating little if any selective mortality with regard to sex.

Movements

Bimonthly distribution patterns were plotted using recapture information from 101 recoveries made during 1979–88, for which recapture location and date were known (Fig. 3). From about March through August recoveries were restricted to the bay, while from September through February a marked pattern of dispersal occurred within and outside of the bay. One shark traveled as far as Elkhorn Slough near Monterey, about 140 km south of the entrance to San Francisco Bay.

To discern year-to-year differences in the temporal and general geographic pattern, Table 4 shows recoveries by year and recapture area (south San Francisco Bay, central and north bays, ocean/outside bay). The year 1983 was unique in that the greatest number of recoveries in any one year was made that year (22 fish, plus 2 fish recovered dead). It was also the only year that ocean recoveries were made as early as September, and the only year when an unusual number of recoveries (6 fish) was made in the central bay in June. (During the 9-year study period, there was only one other instance, in 1981, of a fish being taken in the central bay in June.)

No distribution pattern appeared to be correlated with fish size or sex, but due to the small sample size, the results do not preclude the possibility that the pattern may vary with sexual maturity or age. The sex ratio of fish taken in the ocean was normal (1:1); however, one commercial fisherman, who caught 3 of the 12 tagged fish taken in the ocean, reported that all 3 were gillnetted from the same depression on the sea floor in Half Moon Bay (one taken 13 Nov. 82, the other two taken in 1986 on 20 Oct. and 17 Nov.), and all 3 were large females with developing embryos.

Table 4

Distribution of leopard shark tag recaptures in and around San Francisco Bay, California, by year and area of recapture for which date and recovery area are known.

	Area of recapture			
Calendar year of recapture	South bay	Central & north bays	Outside bay/ ocean	Totals
1979	10	2	1	13
1980	8	9	0	17
1981	11	1	1	13
1982	5	4	3	12
1983	9	9	4	22
1984	9	2	0	11
1985	2	2	0	4
1986	1	0	3	4
1987	2	0	0	2
1988	3	0	0	3
Total	60	29	12	101

Mortality rates and virtual population analysis

The oldest ages reported for this species are 24 years for a male of approximately 135 cm in length and 20 years for a 130-cm female (Kusher 1987, fig. 8). However, we arbitrarily decided to use a maximum age of 30 years in Hoenig's (1983) regression equation since there are records of fish larger (180 cm; Kato et al. 1967) than those that were aged; we also noted that the largest female aged by Kusher (140 cm) was, at 18 years, not the oldest. Because the largest fish cited above was taken prior to the time when there was more than nominal fishing directed at this species, we feel that M may be assumed approximately equal to the Z from Hoenig's regression equation. The result of taking $t_{max} = 30$ in the equation was an estimated M of 0.14.

While we have no explicit estimate of a tag-shedding rate from this experiment, the results of Kato and Carvallo (1967) from multiple tagging of sharks at the Revillagigedo Islands, Mexico, indicated a minimal annual shedding rate of 0.095. We have taken this value, converted it to an annual instantaneous loss rate of 0.10, and added it to the previously estimated 0.14 to obtain $X = M + 0.1 = 0.24$ for use in lieu of natural mortality in the VPA. We assume, and believe it reasonable given the apparent hardiness of the animals and toughness of their skin, that there was no instantaneous (type I) tag shedding.

With regard to the percent of tag recoveries reported to us, we again have no "built-in" estimate, but the California Department of Fish and Game has conducted extensive studies on the return rates for various reward levels associated with tagged striped bass in the same general area that the leopard shark tagging occurred (Stevens et al. 1985). Based on their experience (D. Kohlhorst, Calif. Dep. Fish Game, Stockton, CA 95205, pers. commun., Nov. 1988), it seemed that a 50% reporting rate would be the best value to use as an adjustment for tag recoveries in this case. To utilize this adjustment in the VPA, we use half the actual number of tag releases as the target for convergence.

Table 5

Leopard shark tag recoveries in and around San Francisco Bay, California, including natural mortality (M), estimated fishing mortality (F), and rate of exploitation (E), by post-tagging annual time intervals.

Time interval	Recovery period	Tags recovered	Assumed $M + 0.1$	F	E
1	10/1/79–9/30/80	25	0.24	0.061	0.055
2	10/1/80–9/30/81	18	0.24	0.059	0.054
3	10/1/81–9/30/82	12	0.24	0.053	0.048
4	10/1/82–9/30/83	26	0.24	0.163	0.141
5	10/1/83–9/30/84	13	0.24	0.119	0.105
6	10/1/84–9/30/85	3	0.24	0.038	0.035
7	10/1/85–9/30/86	3	0.24	0.050	0.046
8	10/1/86–9/30/87	5	0.24	0.116	0.103
9	10/1/87–9/30/88	3	0.24	0.099	0.088
	Total	108		$\bar{F} = 0.084$	

Tag recoveries by yearly intervals after the release period, estimated annual instantaneous fishing and natural mortality coefficients, and rates of exploitation are shown in Table 5. Note that these are all of the tag recoveries which could be assigned to the time intervals; other tabulations of recoveries in this paper may differ because of various missing information components.

Yield and stock replacement per recruit

Shown in Figure 4 is the yield-per-recruit isopleth diagram for $M = 0.28$ during the first year of life and 0.14 thereafter. Age at first capture ranges from 4 to 13 years, and F runs from 0.05 to 0.28. The graph indicates a fairly flat yield contour between $F = 0.15$ and $F = 0.28$, with age at first capture between 5 and 10 years.

Also in Figure 4 are isopleths showing percent population replacement per recruit over the same parameters used for the yield computations. For use in calculating population replacement, the fitted curve (Fig. 5) relating Ackerman's data on number of embryos to parental weight was

$$P_t = 22.64 - (7592)\,(0.4208)^{w(t)},$$

where P_t is number of embryos, $w(t)$ is maternal weight (kg) at age t, and the standard error of estimate equals 0.38313. The value for $w(t)$ was obtained from

$$w(t) = 0.00000305 \times \{172.4[1 - \exp(-0.0717[t + 2.302])]\}^{3.05}.$$

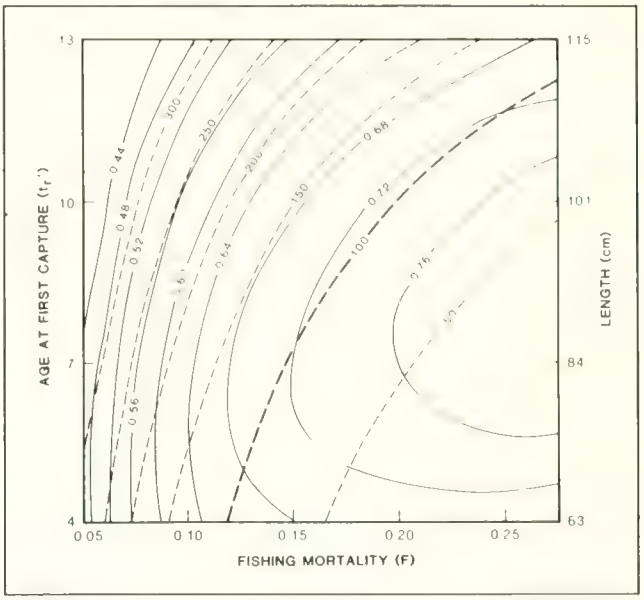

Figure 4

Isopleths showing percent population replacement of leopard sharks tagged in San Francisco Bay, California, in numbers (dashed lines) and yield per recruit in kilograms (solid lines), for $M = 0.28$ during the first year of life and 0.14 thereafter.

Replacement increases steadily as F tends toward 0 and age at first capture increases (equation 2). The shape of this surface is not unexpected, but clearly some type of density-related compensation would be needed to increase mortality or reduce fecundity as the population increases; otherwise in the absence of fishing the sea would be filled with leopard sharks. This mechanism might be in the form of higher juvenile mortality, less frequent litter bearing, or reduced average litter size. Holden (1973, 1977) discusses some possible mechanisms of this type and cites examples from the literature of marine mammals and elasmobranchs. We do not have information to examine any of these possibilities in the present case.

Discussion

If it is assumed that the tagged population approximates the real population, these results suggest that San Francisco Bay leopard sharks are mostly resident, with some moving out of the bay during fall and winter. Judging from the single Moss Landing recovery, limited population exchange evidently occurs between Elkhorn Slough and San Francisco Bay leopard sharks. Also, previously undocumented evidence was received during the course of this study from L. Talent (Oklahoma State Univ., Stillwater, OK 74078, pers. commun., July

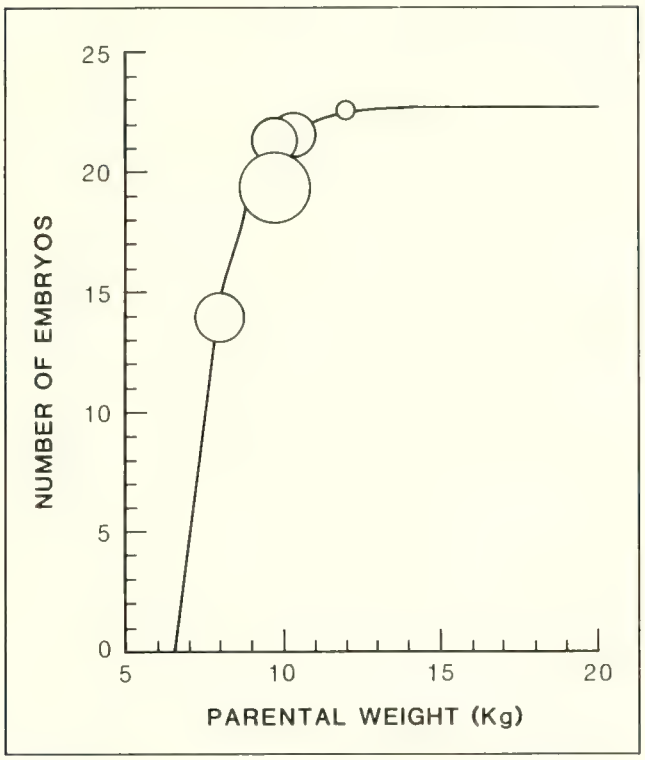

Figure 5

Fitted monomolecular curve relating mean number of leopard shark embryos in litters to parental weight. Areas of symbols are proportional to weighting factors of points used in the fitting process.

1982), who reported that a leopard shark tagged by him in December 1971 in Elkhorn Slough, Moss Landing, California, was recaptured February 1973 in south San Francisco Bay.

It is not known to what extent fishing effort influenced the recapture pattern, because effort information on the commercial and recreational catch is not available to the degree of geographic precision needed for such an analysis. We do know that leopard sharks are susceptible to bottom fishing gear, whether it be baited hook, gillnet, or, to a lesser extent, bottom trawl. Judging from the available data on recreational and commercial landings, and the much greater proportion of recreational versus commercial tag recaptures, recreational anglers are the primary users of the leopard shark resource in northern California. Angling for bottom fishes takes place in most areas inside the bay system year-round (Squire and Smith 1977), although in winter, inclement weather may lower fishing effort within the bay as well as along the open coast. Bottom-fishing effort in the ocean is thought to be comparatively less than in the Bay at least in waters shallower than 91 meters, the reported depth range of this species.

The 1983 peak in the tagged fish recovery rate and the associated rise in fishing mortality that we calculated (Tables 4 and 5) was unexpected. We have no evidence that fishing effort increased that year to cause this jump in the tag return rate, but there was a substantial rise in the California commercial catch of leopard shark that year, primarily driven by an increase in San Francisco landings (Table 1). There was also a similar rise in the estimated recreational catch (Table 2). The year 1983 was also one of unusual oceanographic conditions, when warm, nutrient-poor El Niño water intruded along the central California coast (McClain 1983, Norton et al. 1985). These El Niño conditions may have caused an influx of sharks from more southerly populations, but the increased rate of recovery for San Francisco Bay tagged fish should be independent of immigration of fish from other areas.

The California Department of Fish and Game (1987) and Pearson (1989), conducting trawl surveys of San Francisco Bay fishes, have observed higher trawl catches of leopard sharks during wet as opposed to dry years, and 1983 was indeed a wet year. That year the bay system experienced the highest delta outflows from the Sacramento-San Joaquin River systems in over 10 years, and June freshwater outflows were twice that of the previous wet year of 1982 and six times the previous decade's average outflow for that month (Calif. Dep. Water Resour., DAYFLOW Prog. Summ., Sacramento, CA 95816, Sept. 1987). Perhaps the anomalous conditions affected the local distribution and availability of central California leopard sharks and possibly their benthic prey, making the sharks more vulnerable to centers of fishing pressure.

In estimating the mortality, yield, and stock-replacement values, it was neccessary to make many assumptions and adjustments. Clearly we must assume that the tagged fish rapidly mix with the balance of a relatively closed San Francisco Bay population, and that tagged and untagged animals are equally likely to be caught. But because of the paucity of this type of information on these animals, an apparent high susceptibility of elasmobranch stocks to fishing pressure, and the noticeable increase in fisheries targeting on sharks, we felt it appropriate to present our best estimates based on the available data and current knowledge of elasmobranch biology.

In the case of the leopard shark, high stock maintenance is surely more important than a large yield per recruit. And while there is obviously something wrong with the stock replacement values which exceed 100% on an equilibrium basis, we would like to accept the 100% isopleth as reasonably valid. Noting in Table 5 that estimated F's ranged from 0.038 to 0.163 with a mean of 0.084, and observing in Figure 4 that the 100% replacement isopleth runs well to the right of the

0.68-kg isopleth over the higher observed levels of fishing mortality, it appears that management for full stock replacement would not involve a very great loss of yield per recruit. In fact, assuming an F of 0.2 and an age of first capture of 10 years, which equates to a 100-cm (40-inch) size limit, yield per recruit is less than 10% below the maximum shown in Figure 4. And given any F between the mean estimated value of 0.084 and the maximum estimate of F, the yield with the 100-cm size limit is within 10% of the maximum for that F.

However, in terms of numbers caught per recruit there is a substantial decline as the size limit increases. At $F = 0.2$, numbers per recruit values are 0.126, 0.192, and 0.292 for size limits of 100, 84, and 63 cm respectively; corresponding mean weights of fish comprising the retained catch are 5.8, 4.0, and 2.4 kg. All of these estimates assume that mortalities due to hooking and releasing undersized fish are negligible.

Based on the above information, a viable management strategy for the leopard shark would appear to be a size limit of 40 inches (100 cm). Although this size limit results in a 34% decline in numbers caught compared with a 33-inch (84 cm) limit, the fish which can be kept are almost 50% larger. Further, stock replacement is at the 100% level as compared with only 55% at the smaller size limit.

We stress, however, that our mortality and fecundity estimates were based on data from studies in only one area within the animal's geographic range, and the extent to which these can be extrapolated to the entire coastal population is not known.

Acknowledgments

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Evidence of Survival Value Related to Burying Behavior in Queen Conch *Strombus gigas*

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Interest in queen conch *Strombus gigas* aquaculture and more efficient management of fished stocks has increased due to the declining catches of this species throughout its range (Brownell and Stevely 1981). Knowledge of conch survival is critical to the success of extensive and intensive aquaculture, and also to management of the exploited stocks. Information on survival, including predation rates during the period after larval conch have left the planktonic (drifting) stage and settled onto the bottom until the time they emerge and graze about on the bottom, is very limited.

Despite field searches conducted by numerous researchers in different areas, very few small conch (<1 year-old; ~5 cm in length) have been found in nature (Robertson 1959, Randall 1964, Hesse 1979, Davis and Hesse 1983). Research by Iversen et al. (1986) in the Berry Islands (Bahamas) using a variety of devices to sample the substrate and the substrate-water interface confirmed the paucity of young conch on or near the substrate surface in areas adjacent to aggregations of >1-year-old juveniles. It seems reasonable that these very young conch do not migrate over long distances to the cays where we find the large juveniles, but are carried during their planktonic life by currents to these locations. These findings suggest that conch may be buried almost continuously until they reach a shell length of ~5 cm.

The purpose of this study is to use tag-recapture data to examine the relationship between survival of juvenile conch and their burying activity.

Methods and materials

The data used in this study were collected in the Berry Islands (Bahamas) about 190 km east of Miami, Florida (Fig. 1). A wide range of conch sizes (3.5–22.0 cm) was tagged during these experiments at all seasons and at several different cays to account for the effects of different habitats, conch sizes, and seasonal variation.

The sampling area, consisting of shallow sand flats with abundant turtle grass *Thalassia testudinum*, is described in more detail by Iversen et al. (1987).

Individual conch were tagged with thin, numbered plastic tags affixed to the spire with underwater epoxy. Shell length was taken using a measuring board (Iversen et al. 1987). Shallow intertidal waters were sampled by wading and the deeper offshore water by snorkeling. Counts of tagged conch were made on 23 sampling trips lasting 4–5 days made approximately every 5 weeks between May 1980 and February 1983. A conch was considered to be buried when it was not found on one or more sampling trips, but was found alive on subsequent visits (Table 1). We believe this to be a reasonable assumption, because the aggregations of conch we studied remained in close proximity to the cays and when not buried were easily located. Conchs as large as 10–15 cm in length which we placed in 25-m^2 pens would bury and were not found on some visits despite intensive searching. On subsequent visits a month or more later, they would reappear on the surface of the substrate. For example, of 27 tagged conch in one pen, seven were buried on at least one visit between April and December 1980. Tagged individuals released at various cays that were not subsequently found were considered to have fallen prey to predators; large juveniles ($\gtrsim$16 cm) were assumed to have migrated offshore to deep water (Iversen et al. 1987).

Results

Our tagging data show a significant positive correlation (Fig. 2) between survival and percent buried for conch released in the subtidal region of about–2 m depth south of Vigilant Cay (shell length range, SLR, 3.5–16.5 cm; $r = 0.80$; $P<0.01$), and for conch from intertidal zones at Cat Cay (SLR 4.5–18.0 cm; $r = 0.56$; $P<0.05$) and Little Cockroach Cay (SLR 8.0–22.0 cm; $r = 0.81$; $P<0.05$).

Discussion

Predation is probably the most important cause of natural mortality on stocks of >1-year-old juvenile conch. Based on our searches for parasites in juveniles and adult conch, and our field observations, we do not believe that parasites or diseases play an important role in conch survival. There are reports of isolated mass mortalities of conch

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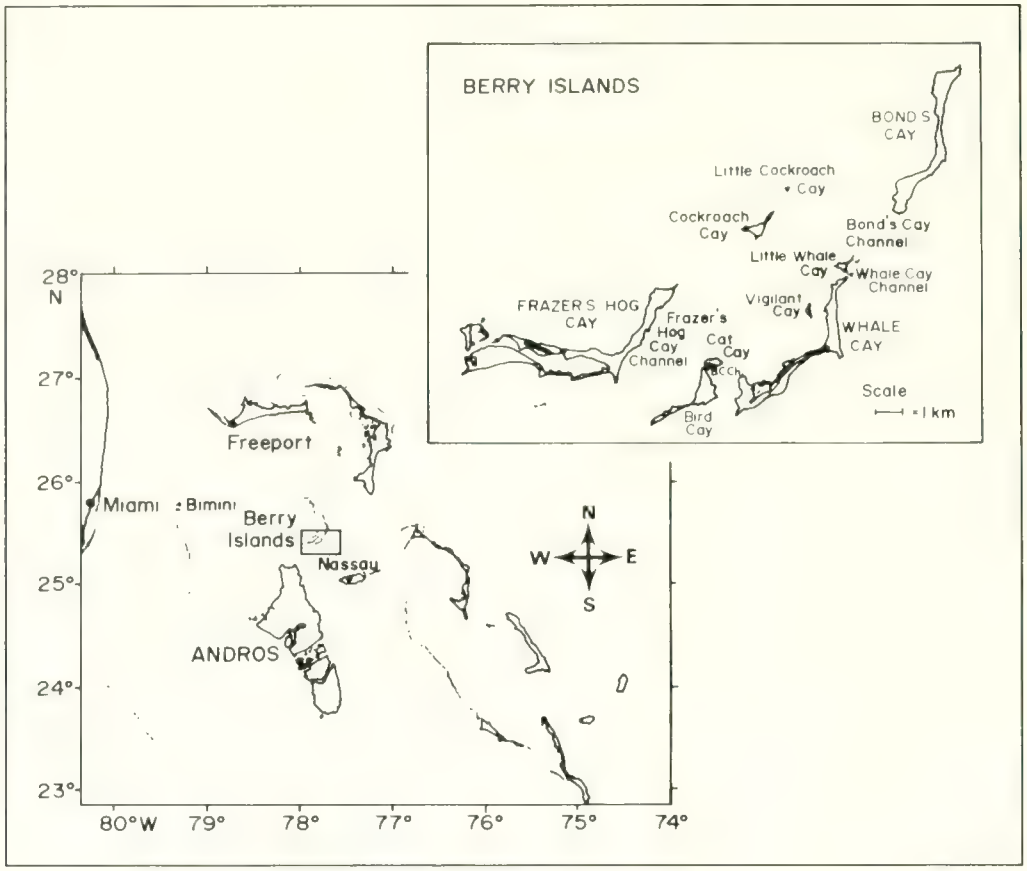

Figure 1

Location of *Strombus gigas* study site in the Berry Island (from Iversen et al. 1987).

Table 1

Example of database used in this study of queen conch burying behavior. Tagging location: Little Cockroach Cay, Berry Islands, Bahamas. Tagging date: 27 May 1980.

	Field observations								
				1980				1981	
Tag no.	05/27	06/23	08/21	09/05	10/03	11/01	12/16	01/23	03/03
0617	14.9	15.3	16.0	(B)	(B)	17.6			
0618	15.8	(B)	(B)	(B)	(B)	(B)	(B)	18.6	
0619	16.5	16.8	17.6						
0620	15.2	15.7	16.6	(B)	17.8				
0621	17.1	(B)	18.1	18.6	19.0				
0622	15.1	15.7	16.6	17.2	(B)	17.7			
0623	16.2	(B)	17.4	17.7	(B)	18.8			
0624	16.7	17.3							
0625	14.7	15.6	16.2	17.0	17.1				
0626	14.4	15.1	15.9	16.4	16.8				
0627	15.2	16.0	16.5	17.4	(B)	18.1			
0628	14.1	(B)	15.3	(B)	16.1	16.0			

A tagged conch is considered to be buried (B) if not found on one or more subsequent trips, but is eventually found. It is assumed to have been killed or to have migrated offshore if not subsequently found. No tags from this group (0617–0628) were found in the vicinity of Little Cockroach Cay during the period February 1981 to the end of the study, February 1983, despite 11 field searches made every 4–6 weeks during this period. Conch of about 18–20 cm shell length generally migrate into deep offshore waters from this cay (Iversen et al. 1987).

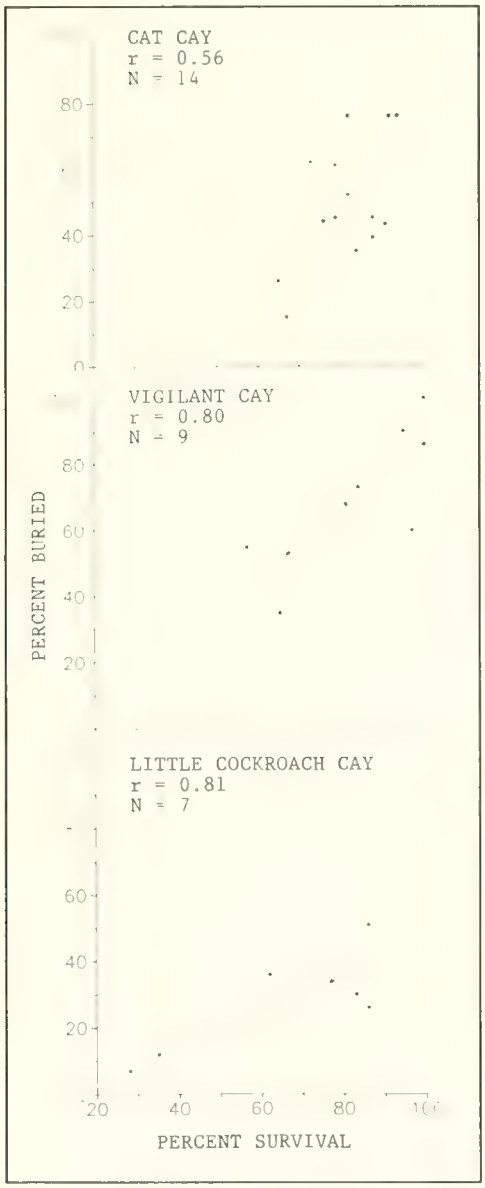

Figure 2

Relationship between *Strongus gigas* burying activity and survival. Vigilant Cay: offshore, 171 conch tagged 3 October 1980; SLR 6.7–9.3 cm. Cat Cay: 455 conch tagged 27 May 1980; SLR 8.9–19.1 cm. Little Cockroach Cay: 84 conch tagged 8 April 1981; SLR 9.2–15.5 cm. N = number of months the experiment lasted.

during the summer on tide flats when temperatures reached extremely high levels (Weil and Laughlin 1984).

In the few trials made to date, survival of hatchery-reared small conch (2.0–7.0 cm in length) released in different locations in the Bahamas and the Caribbean has been extremely low. For example, in St. Croix, Coulston et al. (1987) reported that unprotected juvenile conch did not survive. And in a small-scale preliminary trial, Iversen et al. (1986) reported complete mortality of 1.3–3.7 cm long, hatchery-reared conch placed under protective screens laid on the substrate and held in place by rocks.

To fully interpret our results and put them in context with what is known about mortality and predation in juvenile queen conch, it is necessary to consider the factors affecting both burying behavior and mortality/predation. Concerning the former, we first note that very small conch are almost never found unburied. Although emphasis of our research was on animals larger than 5 cm in length, we searched for small conch during all field trips. Of the 491 small conch (1–9 cm) we found, all but a few (~3%; $N = 15$) were buried, some as deep as 20 cm, while others were barely covered by broken shells and rubble in shallow depressions on a large tidal flat. With only a few exceptions, those found on the substrate were larger than ~5 cm.

Iversen et al. (1987) showed significant differences in burying activity within a tidal cycle at various sites in the Berry Islands. Significantly more conch buried on high tides than on low tides, which they suggested may be a response to possible increased predator activity during high tides when large swimming predators can reach the upper intertidal zone. This apparent tidal-height behavioral response should not be triggered in the deeper (subtidal) water offshore of Vigilant Cay where we released tagged conch. Our results showing a relationship between survival and burying behavior suggest that conch over a wide range of sizes are less vulnerable to predation when buried. This may explain why the highly vulnerable, thin-shelled young-of-year bury for extended periods.

In addition to the effects of conch size and tide stage, burying behavior may be affected by time of year (a proxy which encompasses a number of environmental circumstances, such as water temperature and wind and sea conditions). According to Hesse (1979), seasonal variation in burying behavior is also a factor, with more active burying during the winter when the waters are cooler and the winds stronger than during the remainder of the year. However, no clear-cut seasonal trend in burying activity is evident from our data. Rather, there are generally wide variations in the number of animals buried, which we believe are possibly related to different environmental conditions in the different habitats of the cays where we collected our data. Our size-frequency data suggest that burying activity is not related to the size of the animals, after they attain a shell length of ~5–6 cm.

With respect to mortality, Appeldoorn (1985) showed that juvenile queen conch mortality rates were highest during summer and lowest during winter in Puerto

Rico. Jory and Iversen (1983) found in their studies in the Berry Islands that the highest levels of predation occurred during the summer and the lowest during the winter. They also suggested that reduced mortality in the winter may be due to reduced predator activity and a decrease in conch activity.

Small conch do not grow in length during the winter period of burying (Appeldoorn 1985, Iversen et al. 1986). Therefore, when they emerge in the spring to begin active foraging on the substrate they would have gained no obvious "size" survival advantage as a result of their "hibernation." Johnson et al. (1964) demonstrated that the shell thickness of queen conch increases with activity, and because buried conch would not be expected to be very active during the winter, shell thickness would probably not increase substantially over this time.

Conch survival estimates show trends common to many mollusks: low survival for small animals, increasing as the size of the mollusk increases (Jory et al. 1984; Appeldoorn 1984, 1988; Iversen et al. 1986). Recoveries from 259 tagged wild conchs (SLR 5.0–21.0 cm) at Little Whale Cay, Bahamas, over a 6-month period showed a significant positive correlation between length at tagging and percent recovered ($r = 0.95$; $p<0.05$). This correlation suggests that within this size range mortality decreased with increased conch size. Using floating cages to provide protection from predators and increase survival, we demonstrated that as high as 96% survival was achieved for conch in the size range 5.0–8.0 cm over a 1-year period, while survival of tagged non-caged small conch of similar size after 6 months was only between 0 and 10%. Similar evidence on differential survival by conch size was gathered in Puerto Rico by Appeldoorn (1984) who, by using short-term (~8 weeks) mark-recapture data for both queen conch and milk conch (*S. costatus*), determined that larger individuals suffered less mortality than smaller ones. Jory and Iversen (1988) provided direct evidence of a lack of increase in shell thickness in small juveniles by examining the relationship between shell breaking strength and shell size of queen conch. They found little increase in breaking strength up to a size of ~5.5 cm, suggesting that queen conch shells are relatively thin below this length. Above ~5.5 cm, pressure to crush shells increased rapidly with increasing shell length.

As queen conch increase in size, their spines increase in length and become more robust. Spines may reduce predation on mollusks in various ways (Palmer 1979). They increase the overall size of the shell, thereby limiting predation to larger predators. Conch spines also distribute crushing pressure over a greater area of the shell, thus increasing the pressure required to crush the shell (Jory and Iversen 1988). Spines also serve as additional area for attachment of epibionts which may help conceal mollusks from predators (Feifarek 1987).

The amount of attached organisms on the shells of conch increases with the size of the conch, suggesting a decrease in long-term burying activity with increase in conch size (Iversen et al. 1986). All of the smallest conch we collected had very clean shells with no growth of attached organisms, in contrast to the rapid and heavy growth of algae we observed on the shells of similar-sized conch in hatchery tanks at the University of Miami laboratory and in floating cages at Little Whale Cay, Bahamas. These results further support the hypothesis that young conch spend most of their early life (up to ~1 year of age) below the surface of the substrate, a strategy that may provide haven from some predators (Hesse 1979, Appeldoorn 1985, Iversen et al. 1986).

The relationships between shell size and strength and between survival and burying have practical application in suggesting place and time of year to release hatchery-reared conchs, in order to both minimize predation and increase the efficiency of planting programs using hatchery-reared juveniles of queen conch and several other mollusk species. Placement of young hatchery-reared conch in relatively safe, natural areas optimal for burying and with certain physical characteristics such as strong currents, fine-to-coarse sand, and abundant intact and broken mollusc shells, where red and green algae and sponges occur (as described in Iversen et al. 1986) would obviate the need for overwintering in an expensive hatchery facility. Further, as suggested by Jory and Iversen (1983), fall planting of small hatchery-reared conch would provide time for them to acclimate to their environment before the spring or early summer "emergence." This is particularly relevant in view of evidence available for other mollusk species, where hatchery-reared juveniles are more vulnerable to predators when released in nature than wild juveniles (Tegner and Butler 1985). Development of an inexpensive enclosure for holding large numbers of young-of-the year under the surface of the substrate could further increase survival of hatchery-reared conch juveniles.

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Stomach Contents and Parasite Infestation of School Bluefin Tuna *Thunnus thynnus* Collected from the Middle Atlantic Bight, Virginia*

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In the western Atlantic Ocean, northern bluefin tuna *Thunnus thynnus* are distributed from Labrador and Newfoundland to the Gulf of Mexico, Caribbean Sea, and off Venezuela and Brazil. The northern bluefin tuna is epipelagic and usually oceanic, but seasonally strays near the coast (Collette and Nauen 1983). During June through October, these tuna are common off the eastern United States and Canada (Squire 1962) and support both commercial and recreational fisheries. From the end of May to August, many pods of small school bluefin tuna (<100 kg) migrate past Virginia on their way to more northern feeding grounds. These tuna are caught 30 to 60 km off the Virginia coast in the vicinity of numerous shoals or "hills," by recreational anglers trolling dead bait or lures on or near the surface (Figley 1984). In 1986, 886 boats participated with some degree of regularity in the recreational fishery for tuna and billfish out of Virginia ports (Bochenek and Lucy In press). Further north, there is a recreational fishery for giant (>200 kg) and medium (100–200 kg) bluefin tuna, and, to a lesser extent, school bluefin tuna (Figley 1984).

Bluefin tuna are opportunistic predators that prey upon fishes, mollusks, crustaceans, and salps (Crane 1936; Bigelow and Schroeder 1953; Krumholz 1959; Dragovich 1969, 1970; Mason 1976; Matthews et al. 1977; Holliday 1978). Pacific bluefin tuna *Thunnus thynnus orientalis* caught off California and Baja California preferred the same prey as the Atlantic Ocean subspecies *Thunnus thynnus thynnus* (Pinkas 1971).

The spawning stock of the western Atlantic bluefin tuna has declined sharply since 1970, and both recruitment and juvenile stock size are still substantially lower than in 1970 (ICCAT 1987). Thus, information about life-history characteristics, such as trophic habits, is essential for developing sound management plans for this important commercial and recreational fish. Mason (1976) and Holliday (1978) studied the feeding behavior of school bluefin tuna captured along the eastern coast of the United States; however, only 68 bluefin tuna stomachs were collectively examined from fish caught off or near the Virginia coast (lat 36–38°N and long. 75°W). Therefore, knowledge of the feeding habits of school bluefin tuna off the Virginia coast is relatively sparse. The present paper describes the findings of stomach content analysis for juvenile bluefin tuna collected during the summer of 1986 by recreational fishermen along the mid-Atlantic coast off Virginia.

Methods and materials

During June and July 1986, stomach samples of 97 bluefin tuna were obtained from recreational fishermen as they landed their catch at Rudee Inlet, Virginia Beach, and at Wachapreague on the eastern shore of Virginia. Curved fork length (mm) and the area of capture (Fig. 1) were recorded for each fish. Fish that could not be identified with a specific area of capture were eliminated from the sample. Weights (kg) were recorded for tuna officially weighed on certified marina scales. Stomachs were removed and placed in 10% buffered formalin. Stomachs were opened and designated in the laboratory as either containing food or empty. Stomachs containing only parasites were classified as empty. Stomach contents were rinsed in water and stored in 10% ethanol until identification.

Prey items were sorted into major food groups (fishes, crustaceans, mollusks, and unidentifiable remains), enumerated, and identified to the lowest possible taxon with the aid of a binocular dissecting scope. Volumes were determined by water displacement using a graduated cylinder and measured to the nearest 0.5 mL. Fishes too far digested for certain identification were placed in an unidentified teleost category and used in estimating total prey volume. The majority of unidentified teleost material resembled remnants of sand lance (*Ammodytes* spp.) more than any other recognizable species.

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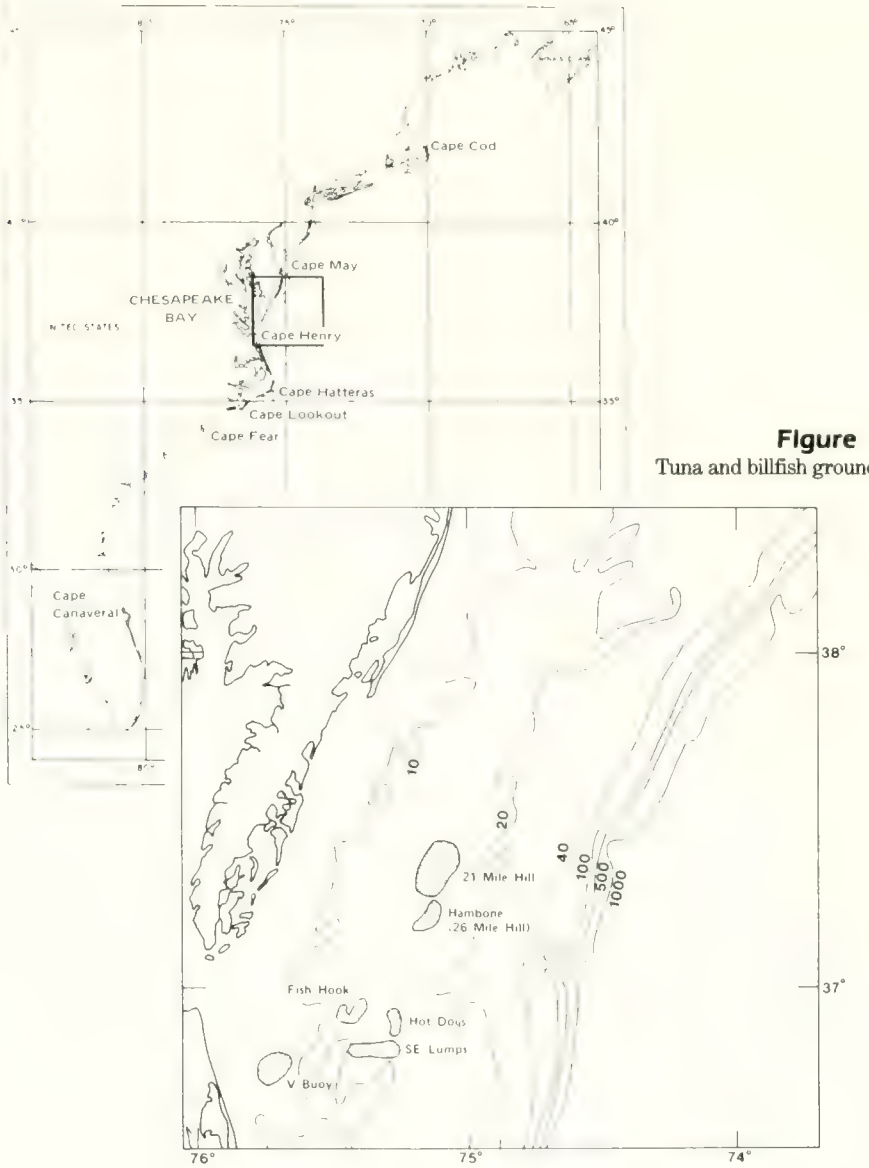

Figure 1
Tuna and billfish grounds off Virginia.

To help evaluate the relationship of the various food items found in stomachs we employed an index of relative importance (*IRI*) (Pinkas 1971):

$$IRI = (N + V) F,$$

where N = numerical percentage, V = volumetric percentage, and F = frequency of occurrence percentage. Percent *IRI* consisted of the *IRI* value of each prey category (unidentified fish and cephalopods excluded) divided by the sum of the *IRI* values (unidentified fish and cephalopods excluded). To determine if the quantity of the key trophic group differed by area of capture (Fig. 1), displacement volume was compared against three areas sampled with a one-way ANOVA model (with displacement volume as the dependent variable and area of capture as the independent factor). The key trophic group was composed of pooled volumetric contributions of both identified and unidentified teleost remains. The three areas were: (1) the "Hot Dog," (2) "'Fish hook" and "S.E. Lumps," and (3) "21 Mile Hill." The "Fish hook" and "S.E. Lumps" areas were pooled because boat captains generally fished both areas during the same trip. The remaining areas, "26 Mile Hill" and "V-Buoy," were both eliminated from the hypothesis test because of low sample sizes ($N = 2$ for both). Significant differences were contrasted by a Student-Neuman-Kuels (SNK) multiple range test set at an experiment-wise error rate (EWER) of 0.05 (Zar 1984). Tests for normality and equality of variance (Zar 1984)

Table 1

List of prey species or class groups occurring in stomachs of juvenile bluefin tuna *Thunnus thynnus* from the Mid-Atlantic Bight, Virginia, 1986.

	No. of individual prey items from 72 stomachs	Percent by number	Volume (mL)	Percent volume	% Frequency of occurrence based on stomachs containing food ($N = 72$)	Index of relative importance (*IRI*)	% *IRI*
Teleosts							
Ammodytes spp. (sand lance)	403	84.1	1028.0	30.75	48.6	5583.2	0.968
Peprilus triacanthus (butterfish)	11	2.3	84.0	2.51	2.8	13.5	0.002
Hippocampus erectus (lined seashore)	9	1.9	2.5	0.07	1.4	2.7	0.0004
Aluterus scriptus (scrawled filefish)	1	0.2	1.5	0.04	1.4	0.4	0.00006
Unidentified teleosts (primarily sand lance)	NA	NA	1653.5	49.46	75.0	NA	NA
Cephalopods							
Lolliguncula brevis (Atlantic brief squid)	48	10.0	432.0	12.92	6.9	158.3	0.027
Loligo pealeii (longfin squid)	2	0.4	124.0	3.71	2.8	11.6	0.002
Unidentified cephalopods	NA	NA	5.0	0.15	1.4	NA	NA
Miscellaneous							
Salpidae			12.3	0.37	8.3	NA	NA
Idotea sp. (Isopod)	5	1.0	0.5	0.01	1.4	1.5	0.0002
Totals	479		3343.3			5771.0	1.0
Total stomachs analyzed	97						
No. (%) containing food materials (identified and unidentified)	72(74.2)						
No. (%) empty	25(25.8)						

indicated that the logarithmically transformed volumes were appropriate for ANOVA.

Results

Food analysis

Of the 97 juvenile bluefin tuna stomachs examined, 72 (74%) contained food. These tuna averaged 21.3 kg ($n = 7$, SD 7.7, range 15–39 kg) with a mean fork length of 90 cm ($n = 85$, SD 13, range 70–132 cm). Stomach contents consisted of two primary food groups: teleosts and cephalopods. Teleosts contributed over five times the percent volume to the diet (82.8%) compared with cephalopods (16.8%) (Table 1). Teleosts occurred in 91% of those stomachs containing food items and accounted for 86% of the total identified prey items (Table 1). Major subgroups of identifiable teleosts by percent frequency of occurrence (based on number of stomachs containing food), *IRI*, and percent *IRI*, listed in decreasing order were sand lance, butterfish *Peprilus triacanthus*, lined seahorse *Hippocampus erectus*, and scrawled filefish *Aluterus scriptus* (Table 1). Sand lance was the predominant teleost occurring in stomachs, especially considering that the unidentified teleost category (probably primarily sand lance) contributed the greatest volume of all prey species found (Table 1).

Cephalopods occurred in 14.4% of those stomachs containing food (Table 1). This group was represented by two species, the Atlantic brief squid *Lolliguncula brevis* and the longfin squid *Loligo pealeii*. Unidentified cephalopod remains accounted for the lowest percent volume (0.2%) of prey items in stomachs containing food, whereas Atlantic brief squid contributed the highest (12.9%) (Table 1).

A third, miscellaneous prey category included salps and one immature species of isopod. A cigarette wrapper and piece of *Sargassum* weed were each present in two of the stomachs.

The combined volumetric contributions of teleost remains to the gut were significantly affected by area of capture (ANOVA; $F = 8.93$, df 2, 82, $P < 0.0003$). Stomach contents of tuna landed from "21 Mile Hill" had significantly higher volumes of teleost remains than did stomachs taken from either the "Hot Dog"

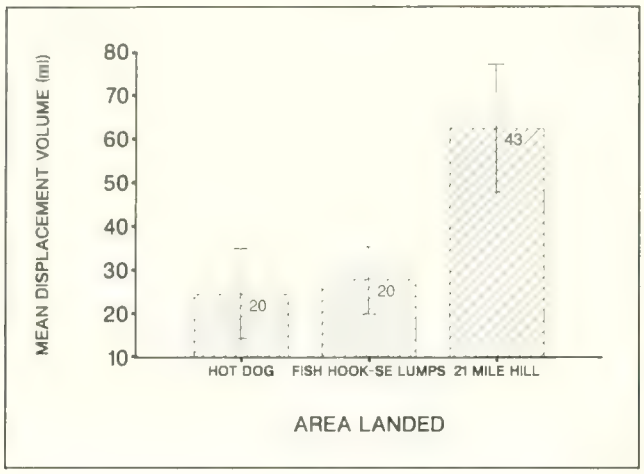

Figure 2

Mean combined displacement volume of identified and unidentified teleost remains from stomachs of bluefin tuna collected from three different areas off Virginia. Numbers within each bar indicate number of specimens sampled; vertical lines indicate ±1 SE.

or "Fish hook and S.E. Lumps" areas (SNK: EWER 0.05) (Fig. 2).

Digenetic trematodes *Hirudinella ventricosa* were found in 8 (11.1%) of the stomachs and averaged 10 mm in length and 2–3 mm in width. The worms were never attached to the lining of the stomach and were typically found at the posterior end. The number of worms per stomach ranged from 1 to 2 with a mean of 1.14 *H. ventricosa* per individual stomach. The possible effects of area landed on the number of trematodes occurring in the stomachs were not evaluated because of the relatively low rate of parasitism.

Discussion

Diet

This study indicates that school bluefin tuna, captured off the Virginia coast, feed predominantly on the sand lance. Mason (1976) was the first to report sand lance as a prey item of school bluefin tuna caught off the U.S. East Coast. He also reported sand lance to be the most important prey of school bluefin tuna caught off Virginia, but for fish taken north of Virginia, mackerel (*Scomber* spp.) replaced sand lance as the dominant prey. Holliday (1978) also found the sand lance to be the predominant food item for bluefin tuna captured by trolling along the U.S. East Coast. The *IRI* of sand lance in this study (*IRI* = 5583) is very similar to that reported by Holliday (1978) (*IRI* = 4896).

Sand lance form dense schools over New England and mid-Atlantic Continental Shelf areas. They occur throughout the water column during daylight hours, and are available to tuna predation at various depths (Meyer et al. 1979, Auster and Stewart 1986). Tuna predation on sand lance may affect the populations of this important forage species off Virginia. Reproducing populations of sand lance, as indicated by egg and larvae counts, exist on the Virginia shelf (Norcross et al. 1961); hence, the Virginia coast is an important habitat to the species. The sand lance serves as an important link between secondary producers and higher trophic-level fish and mammals in marine food chains (Bigelow and Schroeder 1953); thus, extensive predation by tuna could affect marine mammal populations. A cause-and-effect relationship may exist between low mackerel and herring stocks (resulting from heavy fishing mortality) and the observed population explosion of sand lance larvae in the mid- to late 1970s (Sherman et al. 1981); thus, tuna predation on sand lance could be beneficial to the return of mackerel and herring stock abundance.

The Atlantic brief squid was the second most important item consumed by school bluefin tuna examined in our study. Mason (1976) found two squid in the 20 fish he examined from Virginia waters. Holliday (1978) also reported similar species of cephalopods in stomach contents of the bluefin tuna taken off the U.S. East Coast. Krumholz (1959), working near the Bahamas, reported salps as the second most important food item. In the western North Atlantic, Dragovich (1970) noted molluscs (mainly cephalopods) as second in trophic importance. Similarly, Matthews et al. (1977) also reported cephalopods, pteropods, and heteropods as being the most frequent invertebrate forage group after fishes. For California bluefin tuna, the second most important food item was the California market squid *Loligo opalescens* or the pelagic swimming crab *Pleuroncodes planipes*, depending upon the area of capture (Pinkas 1971).

The butterfish, lined seahorse, and scrawled filefish were found in very few stomachs, being rare contributors to the diet of bluefin tuna in this study. These prey species demonstrate considerable diversity in their foraging locations, including nearsurface, mesopelagic, and demersal habitats. It is possible that the butterfish, lined seahorse, and scrawled filefish are associated with drifting *Sargassum* weed; thus, tuna may feed in part around drifting *Sargassum* communities. Other miscellaneous items found in the stomachs were salps, the isopod *Idotea* spp., a cigarette wrapper, and *Sargassum* weed. Holliday (1978) also reported the occurrence of *Idotea* spp. in stomachs of bluefin tuna caught trolling near *Sargassum* communities. He hypothesized that the isopod and *Sargassum* weed were accidently ingested by the tuna while pursuing other prey.

Parasites

The digenetic trematode *Hirudinella ventricosa* occurred in 11% of the stomachs examined in this study. Mason (1976) also found an annulated hemiurid trematode in 2% of the bluefin tuna stomachs he examined from the western Atlantic Ocean. The trematodes in Mason's (1976) study were found in both empty stomachs and stomachs which contained food. Crane (1936) reported *Distoma*-like worms in 25% of giant bluefin tuna stomachs he examined off Maine. *Hirudinella ventricosa* (= *marina*) occurred in 9% of school bluefin tuna and 48% of giant bluefin tuna stomachs collected from North Carolina to Massachusetts (Holliday 1978).

Giant trematodes of the genus *Hirudinella* frequently parasitize scombroid fishes (Nigrelli and Stunkard 1947, Nakamura and Yuen 1961, Watertor 1973, Manooch and Hogarth 1983). Adult parasites typically attach to the stomach lining and remain near the site of attachment throughout this life-stage (Manooch and Hogarth 1983). These digenetic endoparasites have complicated life cycles involving an alternation of generations and hosts; however, the life cycle of *Hirudinella* spp. is still unknown (Manooch and Hogarth 1983).

Attempts to evaluate the incidence of parasitism by size and sex of the host and by geographical area of collection have demonstrated mixed results (Nakamura and Yuen 1961, Manooch and Hogarth 1983). Nakamura and Yuen (1961) examined the occurrence of the parasite *H. ventricosa* (= *marina*) in the stomachs of skipjack tuna *Euthynnus pelamis* collected from Hawaii and off the Marquesas. They concluded that significant differences in the occurrence of trematodes collected from these two areas were attributable to time (year of collection) rather than area. Manooch and Hogarth (1983) reported distinct differences in the incidence of parasitism by *H. ventricosa* between wahoo *Acanthocybium solanderi* from the coast of Florida-South Florida and wahoo from the rest of the southeastern Atlantic. They suggested that this difference may reflect two subpopulations of wahoo along the southeastern U.S. coast: a northern population characterized by high incidence of trematodes, and a southern population with a much lower incidence.

Watertor (1973) examined 258 bluefin tuna captured off the East Coast of the United States (lat. 35–40°N; long. 65–75°W) and off the northeast coast of South America (lat. 0–18°N; long. 50–82°W). Of these, 51 were infected with *H. ventricosa* (= *marina*), nearly twice the infection rate noted in this study. There are two possible explanations for this difference. First, the parasites described by Watertor (1973) were pooled from both the eastern U.S. and northeastern South American samples. Inclusion of a South American group, with possibly a higher prevalence of parasitism, similar in nature to that described for wahoo by Manooch and Hogarth (1983), might have biased the values reported by Watertor (1973). Secondly, Watertor (1973) did not report the overall size ranges of bluefin tuna used in his study. Inclusion of giant bluefin tuna, with a higher prevalence of parasitism (see Crane 1936) may also contribute to apparent differences in levels of infection.

Area effects

Environmental factors such as temperature and oceanographic frontal zones have been shown to markedly influence the distribution, abundance and catchability of tunas (Murphy 1959, Uda 1973, Laurs and Lynn 1977, Rockford 1981, Sund et al. 1981, Laurs et al. 1984). Murphy (1959) suggested that the aggregation of albacore *Thunnus alalunga* in clear water on the oceanic side of fronts in nearshore areas may reflect an inability to efficiently capture large, mobile prey in turbid coastal waters. This same mechanism may help to explain the higher combined displacement volumes of sand lance and unidentified teleost remains in the stomachs of tuna taken from the "21 Mile Hill" compared with the "Hot Dog" or "Fishook and S.E. Lumps" areas (Fig. 2). Turbidity associated with effluent from Chesapeake Bay might have reduced the ability of bluefin tuna to detect mobile forage such as the sand lance and other teleosts. The effluent from the Chesapeake Bay appears in shelf waters as a lens of freshened water (with high concentrations of bay water constituents) extending offshore and towards the south as a part of the general shelf circulation (Ruzecki 1981). The three areas in question are directly offshore of the Chesapeake Bay mouth (Fig. 1). Differences in the diet of bluefin tuna have also been attributed to depth of capture, availability and type of food in a given area, time of day or year, spawning, atmospheric conditions, physiological conditions of predator fish, size of prey, and size of the bluefin tuna (Dragovich 1970).

We conclude that the sand lance is the most important forage of school bluefin tuna off the Virginia coast and suggest that this prey species, as well as teleosts in general, may become more vulnerable to tuna predation in areas least affected by the turbid waters of the Chesapeake Bay plume. In addition, the occurrence of the digenetic trematode *Hirudinella ventricosa* in a small but significant number of bluefin tuna off Virginia suggests that variation in infestation rates of this parasite might provide a mechanism to help distinguish among possible subpopulations of bluefin tuna occurring in the Western Atlantic.

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Horizontal and Vertical Movements of Pacific Blue Marlin Captured and Released Using Sportfishing Gear*

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Despite the commercial and recreational importance of Pacific blue marlin *Makaira nigricans*, little is known about their biology or behavior. This is due mainly to their large size and pelagic habitat and the difficulty in maintaining them in captivity or observing their behavior in the wild. However, two techniques are available to elucidate their movements: capturing and releasing marlin fitted with identification tags, and tracking of fish carrying ultrasonic transmitters.

The recovery of tagged marlin has enhanced our understanding of the long-term geographical range of individual fish and their minimum rates of travel (Squire 1974, Squire and Nielsen 1983, Bayliff and Holland 1986), and growing interest in the tag and release of marlin by sportfishermen should produce an increasingly precise picture of marlin movements. However, this technique cannot answer questions regarding the vertical movements of marlin, and questions remain concerning both the survival of tagged fish following the trauma of capture and the nature of their behavior immediately upon release.

Fine-scale observations of the horizontal and vertical movements of pelagic fish can be obtained for periods of up to a few days by tracking fish equipped with depth-sensitive ultrasonic transmitters (Holland et al. 1985, 1990; Bayliff and Holland 1986). For billfishes, this technique has been used to track swordfish *Xiphius gladius* (Carey and Robison 1981) and striped marlin *Tetrapturus audax* (Holts and Bedford In press). Similarly, Yuen et al. (1974) tracked Pacific blue marlin but used temperature-sensitive transmitters to monitor ambient water temperature from which depth was later calculated using bathythermograph data. However, this study heightened concerns about tagging mortality rates because three of the five tagged fish died soon after release.

Here we report on the movements of six Pacific blue marlin tracked in the waters around the Hawaiian Islands. Of particular interest were survivorship and behavior of the fish immediately upon release, their patterns of vertical movement, and their overall patterns of horizontal movement. To discern any common patterns of movement associated with one particular area of ocean, three fish were caught and tracked from one well-defined location on the Kona coast of Hawaii. For comparison, two other tracks were initiated several miles away along the same coast, and one marlin was tracked off the Waianae coast of Oahu.

Methods

The ultrasonic tracking techniques employed were identical to those used previously to track yellowfin tuna (Holland et al. 1985, 1990; Bayliff and Holland 1986). The transmitters used in the present study had a nominal life span of 3 days and a maximum working pressure of 500 psi (Vemco, Halifax County, Nova Scotia). The signal, encoding depth information by variable pulse interval, was recorded on audiotapes for later onshore plotting of vertical movements of the fish. Horizontal location was determined every 15 minutes (or more frequently when necessary) by using a combination of Loran-C, radar, visual, and bathymetric fixes. Water temperature was measured by expendable bathythermographs deployed approximately every 3 hours.

Aggregate depth and temperature distributions were calculated (with 10-m and 1°C bins, respectively) as percentages of the total track time spent at any particular depth or temperature. For temperature, the combined distributions of all fish were calculated as the percentage of time spent in the various temperature strata relative to the upper mixed layer.

Each transmitter was attached with a 10-cm length of 130-lb test monofilament to a stainless steel "arrowhead" ($\sim 2.75 \times 1.75 \times 0.1$ cm; Fig. 1) modified from the type

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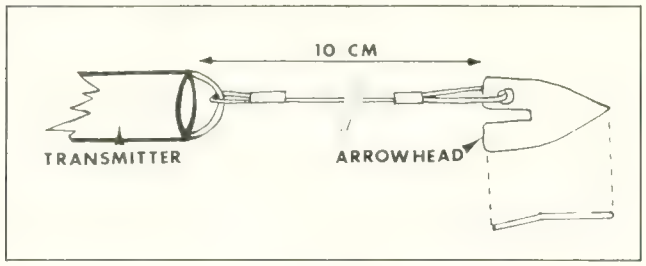

Figure 1

Tag attachment system for Pacific blue marlin. A stainless steel arrowhead, with downcurved tines and central notch to accommodate the prong of the applicator pole, is attached to the transmitter body with a 10-cm length of 130-lb test monofilament crimped in two places.

used by Yuen et al. (1974) and Carey and Robison (1981). The arrowhead fitted into the tip of a standard tagging pole to which the transmitter was loosely bound with rubber bands (Yuen et al. 1974, Holland and Bayliff 1986). The fish was harpooned in the trunk musculature, thereby allowing the transmitter to lie against the surface of the fish alongside the forward half of the dorsal fin. Once the transmitter was attached, the fish was released by cutting the leader, leaving the hook in place.

Fish were caught by surface trolling with artificial lures and standard sportfishing rods and reels. Two of the fish were caught on the tracking research vessel *Kaahele'ale*, and four were caught by teams participating in the 1988 and 1989 Hawaii International Billfish Tournaments (HIBT). In these latter cases, the transmitter and applicator pole were passed to the anglers' vessels during the fighting of the fish. Crew members then tagged the fish while the tracking vessel stood by ~100 m away. Once the fish had been released, tracking began.

To replicate tracks from one well-defined area, three tracks were initiated on the fishing grounds off Keahole Point, Hawaii. This is an area approximately 5 nautical miles (nmi) long and 2 nmi wide that is renowned for high catch rates of marlin during certain periods of the summer. For comparison, two other tracks were initiated from locations ~12 nmi south of the Keahole grounds, and one fish was tracked off Barbers Point, Oahu.

Results

Six Pacific blue marlin were tracked. The three Keahole fish were all caught within a 1-nmi radius over a span of 19 days in 1988; one track was 24 hours, and two were of 42 hours duration each (Fig. 2). In 1989,

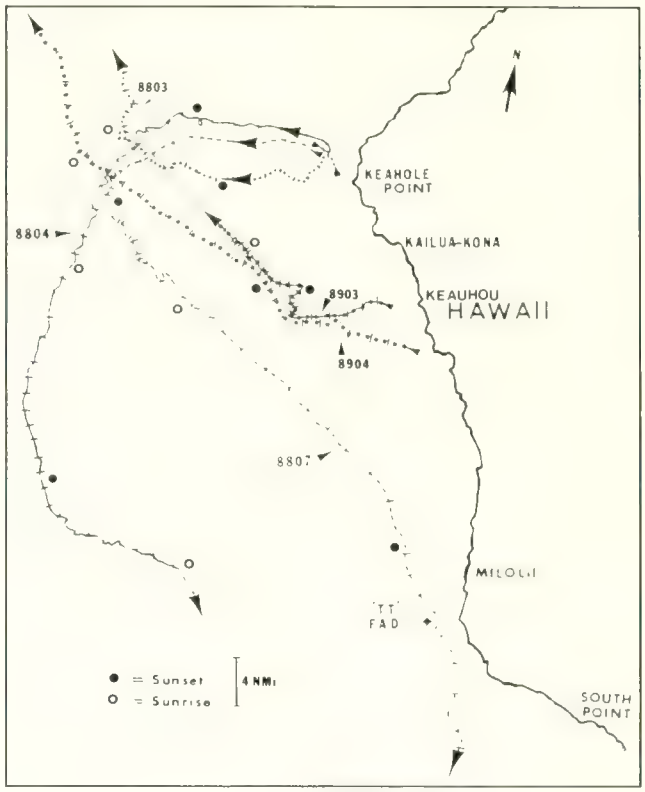

Figure 2

Horizontal movements of five Pacific blue marlin tagged off the Kona coast of Hawaii: three off Keahole Point and two off Keauhou. Lines perpendicular to the tracks represent hourly positions.

over a period of 4 days, two marlin were tracked from starting points ~4 nmi apart off Keauhou and were tracked for 26 and 29 hours (Fig. 2). The Barbers Point fish was tracked for 7 hours. Thus, all fish survived for at least 7 hours after release, and there is no reason to believe that any of the fish subsequently died as a result of the capture and tagging procedure.

Synopsis of tracks

Fish 8710 (weighing ~150 kg) was caught on a single-hooked artificial lure trolled behind the tracking vessel *Kaahele'ale* at a location 7 nmi west of Barbers Point, at 0904, 18 October 1987. After a fight time of 30 minutes, the fish was brought to the side of the boat. The fish was cleanly hooked through the bill and was immobile. The transmitter was embedded dorsolaterally, about a third of the way back along the dorsal fin. After release, the fish glided downwards and away from the boat and swam away on a southwesterly (offshore) course, which it maintained for the duration of the track. After 7 hours the fish was lost while at the surface. Data on the rate of horizontal movement for

Table 1

Rates of horizontal movement of captured and released Pacific blue marlin off Hawaii.

Track ID	Duration (hr)	Average speed (kn ± SD) Day	Night	Total	First hour
8710	7.0	1.21±0.27	NA	1.21±0.27	1.50
8803	24.0	1.48±0.31	1.37±0.32	1.43±0.30	1.20
8804	42.0	2.04±0.43	1.78±0.37	1.90±0.42	3.25
8807	42.0	2.25±0.67	2.09±0.67	2.18±0.65	3.25
8903	26.0	0.95±0.54	0.65±0.36	0.83±0.49	1.80
8904	29.0	1.62±0.37	1.68±0.39	1.65±0.37	3.00

this fish and the other five marlin are summarized in Table 1.

In terms of vertical behavior, this fish dove when released and spent the next 4 hours in the top 3 or 4 degrees of the thermocline at depths varying between 50 and 70 m. The fish then moved closer to the surface, spending 92% of the last 3 hours of the track within the surface mixed layer, moving between the surface and 35 m.

Fish 8803 (60 kg) was caught and tagged 2 nmi off Keahole Point at 1120, 8 August 1988, by a team participating in the HIBT. The fish was fought for ~20 minutes and described as tired but in good condition when released by the anglers. This marlin moved steadily west for ~12 hours before curving north during the night (Fig. 2). The fish was moving northwest when the track was terminated after 24 hours because of deteriorating sea conditions. The vertical movements of this fish (Fig. 3A) had a consistent "floor" where

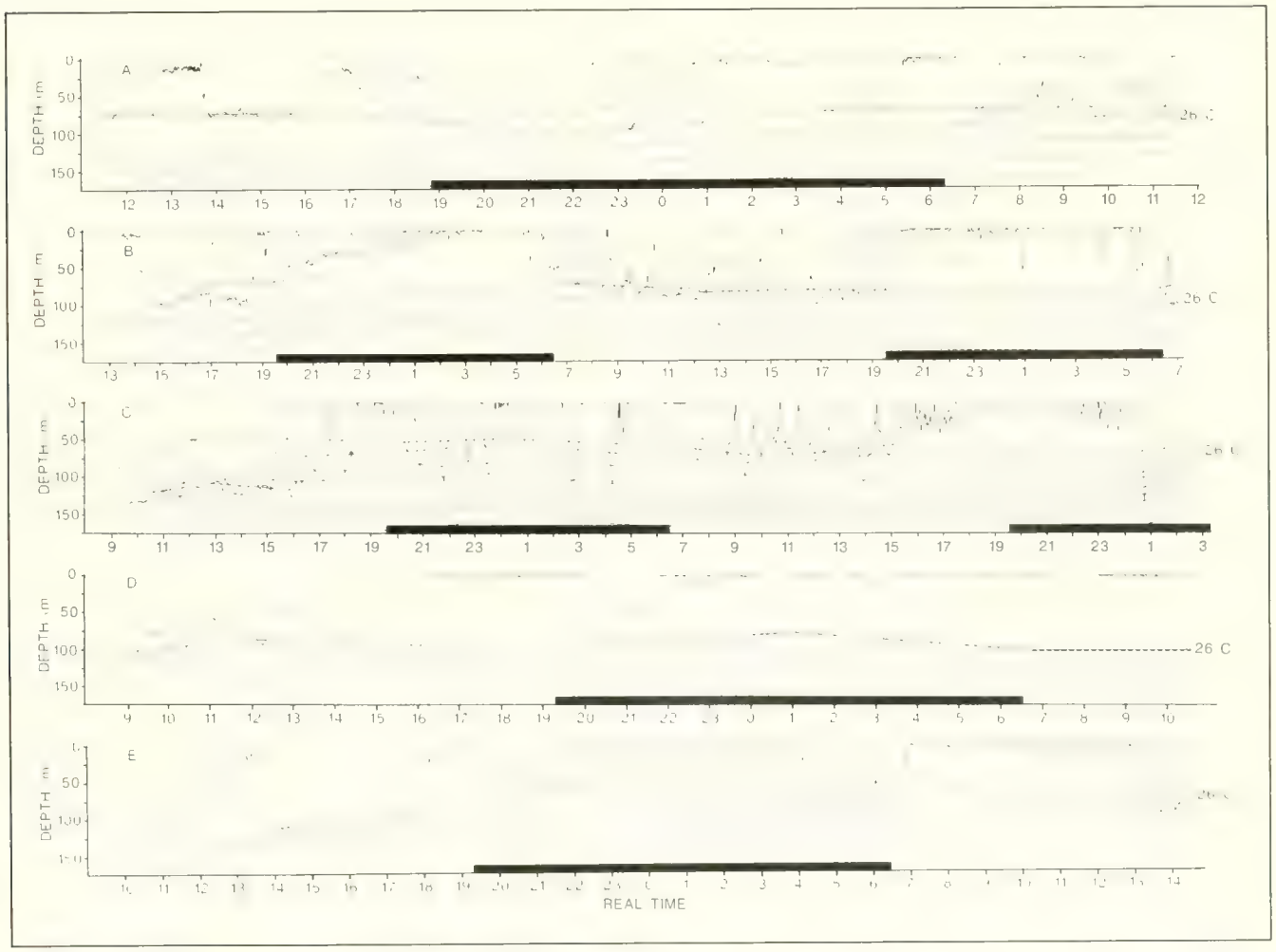

Figure 3

Vertical movements of marlin tracked off Keahole Point and Keauhou, Hawaii. A = fish 8803; B = 8804; C = 8807; D = 8903; E = 8904. Solid horizontal line represents the sharpest inflection in water temperature at the bottom of the mixed layer, whereas dashed horizontal lines represent 1°C isotherms, starting at 1°C below surface temperature. Horizontal bars represent nighttime.

the surface mixed layer met the top of the thermocline at depths varying between 75 and 100 m. During the daytime, the fish moved in and out of the top of the thermocline, with occasional excursions towards the surface; during the night, movements were more completely confined within the mixed layer with more time spent very close to the surface.

Fish 8804 (also estimated to weigh 60 kg) was caught and tagged by an HIBT team at 1310, 11 August 1988, 3 nmi off Keahole Point. Fight time and release condition were similar to fish 8803. After an initial, brief movement towards shore, this fish also proceeded directly west for about 8 hours before curving southward after sunset on the first night (Fig. 2). This direction was maintained all day during the second day until after sunset when it turned more shoreward. However, a southerly course was resumed after sunrise of the third day. The track was terminated after 42 hours.

The daytime vertical movements of this fish were focused around the interface between the mixed layer and the thermocline. From that depth (around 90 m) intermittent excursions were made to the surface. Nighttime distribution was shifted markedly towards the surface (Fig. 3B).

Fish 8807 was caught by the *Kaahele'ale* at 0900 on 27 August 1988, 3 nmi off Keahole Point. The fish, which was fought for 35 minutes, was caught using an artificial lure with a single hook that lodged in the base of the marlin's bill. The fish, weighing in excess of 160 kg, was completely immobile and floating belly-up at the side of the boat when the transmitter was attached near the midline in line with anterior insertion of the anal fin.

When the leader was cut, the fish sank slowly upside down under the boat but, after ~30 seconds, righted itself and began to swim slowly downwards. During the next hour, the fish traveled 3.25 nmi and, as with the previous two Keahole fish, headed steadily west, in this case for 7 hours. After sunset, the fish slowed and assumed a southeasterly course which it retained for the remainder of the track. After sunset on the second night, the fish returned close to the island and briefly visited fish aggregating device (FAD) TT off Milolii (Fig. 2). The fish was lost in rapidly deteriorating sea conditions off South Point, Hawaii, after 42 hours of tracking. At this time, the fish appeared to be continuing in a southerly direction.

Immediately upon release, this fish descended into the uppermost 2 or 3 degrees of the thermocline, where it remained for 6 hours as it swam steadily offshore. Upward excursions towards the surface started 3 hours before sunset, and movements on the second day were mostly in the thermocline-mixed layer interface with frequent upward movements, some of which reached the surface. As with the other Keahole marlin, nighttime distribution was shifted towards the surface, with considerable amounts of time spent at the surface (Fig. 3C).

Fish 8903, weighing ~75 kg, was caught and released 3 nmi off Keauhou Bay by a team in the 1989 HIBT. The fight time was ~20 minutes and the fish was lively when the transmitter was attached. Immediately upon release, the fish headed offshore for 5.5 hours before turning north (Fig. 2). This initial deviation in direction occurred ~11.5 nmi offshore and coincided with the marlin's first movement to the surface from the top of the thermocline, where it had been since the initial release (Fig. 3D).

Compared with other fish tracked in this study, this fish spent large amounts of time swimming slowly very close to the surface, often with the tips of its dorsal and caudal fins protruding above the surface. Although this "lazy" surface behavior is not uncommonly observed by fishermen, this was the only fish to demonstrate this behavior in the current study. The track was terminated after 24 hours, with the fish continuing to swim slowly at the surface in a northwesterly direction.

Fish 8904, also weighing ~75 kg, was caught and released by an HIBT team at a location ~2 nmi offshore of Kealakekua Bay, after a 36-minute fight. This fish also ran west (for ~6 hours) to a point 11.5 nmi offshore, at which time contact was lost for ~2 hours. When relocated, the fish had adopted a northwesterly course which it maintained for the remainder of the 29-hour track (Fig. 2). Vertical movements were similar to those of other fish, being largely constrained by the top of the thermocline and the surface, and averaging closer to the surface at night than during the day (Fig. 3E).

Temperature and depth distribution

Pooling the data from all six fish indicates that 82% of the daytime and 97% of nighttime distribution occurred in the mixed layer and top 2 degrees of the thermocline. In terms of depth, approximately 36% of the daytime and 60% of nighttime was spent between the surface and 30 m, the rest of the time being spent at greater depths (Fig. 4).

Discussion

Although the sample size reported here is quite small, these data represent a significant increase in the number of Pacific blue marlin tracked. Also, several aspects of the behavior of these marlin show remarkable consistency.

For instance, the behavior of all the fish tracked in this study was strongly influenced by the interface

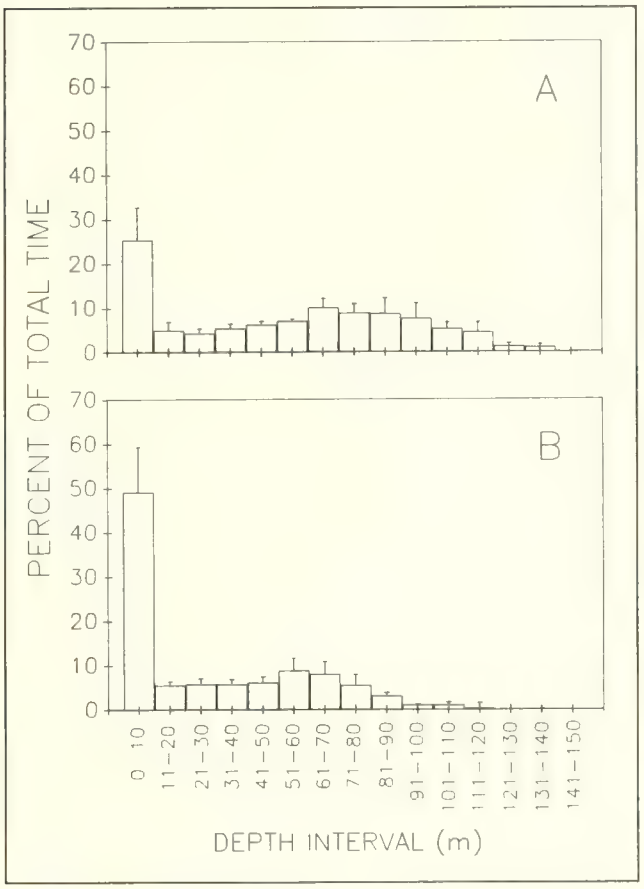

Figure 4
Aggregate depth distribution of six Pacific blue marlin off Hawaii during daytime (A) and nighttime (B).

between the surface mixed layer and the top few degrees of the thermocline, even though the depth of this interface varied between tracks. Unlike yellowfin tuna *Thunnus albacares*, which are also associated with this feature (Carey and Olson 1982, Yonemori 1982, Holland et al. In press), the marlin only rarely dove below the top of the thermocline. Thus, a major portion of the distribution of these marlin was bracketed by the surface and the bottom of the mixed layer. This behavior—not making deep dives, and spending most time in the mixed layer and upper thermocline—is similar to that of striped marlin tracked off California (Holts and Bedford In press), but differs greatly from that of swordfish which make frequent deep dives into cold water (Carey and Robison 1981). Compared with the striped marlin tracked off California, most of the blue marlin in Hawaii spent a relatively small amount of time very close to the surface. This may be due to the shallower depth of the thermocline off California (15–25 m) compared with Hawaii (35–90 m). With the exception of fish 8903, which spent an atypical amount of daytime very close to the surface, the marlin tracked in the present study moved closer to the surface at night. This differs from the striped marlin data, but is consistent with the behavior reported for skipjack tuna *Katsuwonus pelamis* (Yuen 1970), swordfish (Carey and Robison 1981), yellowfin tuna (Yonemori 1982, Holland et al. In press), and bigeye tuna *T. obesus* (Holland et al. In press).

Upon release, all six marlin dove into the upper layers of the thermocline and remained there for several hours. Onset of consistent upward excursions from the thermocline appeared to represent the end of the post-capture recovery period, usually between 4 to 6 hours. The recovery period was initiated by comparatively high-speed swimming, with four of the six fish travelling farther in the first hour following release than at any other time during the tracks. Because marlin are obligate ram-ventilators, these fish may be swimming fast enough to repay the anaerobic metabolic debt incurred during the fight, but not so fast as to acquire new debt. The fast speeds of the first hour are even more remarkable considering that at least two of the fish appeared to be completely exhausted when tagged and released. Holts and Bedford (In press) also report deeper than normal depths and heightened activity levels immediately upon the release of striped marlin.

With the exception of slow-moving fish 8903, the range of swimming speeds of individual fish in our study (1.2–2.18 kn) are similar to the blue marlin (1.2–1.9 kn) of Yuen et al. (1974). This is somewhat faster than the striped marlin speeds (0.75–1.45 kn) observed by Holts and Bedford (In press). In the present study, most of the fish swam slightly slower at night than during the day.

One of the most remarkable features of the current study is the consistent direction of movement displayed by the marlin in the first several hours of each track. Even though the three Keahole fish could have moved anywhere within a 240°-sector without running into land, all three swam along parallel westerly courses that took them directly offshore. Also, initial deviation from these parallel tracks occurred in the same general area ~12 nmi offshore. Similarly, both fish caught off Keauhou swam offshore for ~6 hours along almost identical paths, and both made their first major directional changes between 11 and 12 nmi offshore. This point in these two tracks was separated by only ~0.5 nmi, even though the release sites were over 4 nmi apart. The previously longest track of a Pacific blue marlin (22.5 hours; Yuen et al. 1974) was also initiated off Keauhou, and also commenced with a 7 nmi-movement offshore, as did the Barbers Point marlin tracked in the current study.

These results suggest that direct movement offshore may be a common response to the trauma associated

with capture and release. The first major horizontal direction changes often coincide with changes in vertical behavior and may represent the end of the recovery period.

Previous blue marlin tracks, and those acquired in the present study, share the characteristic of essentially straight or slowly curving azimuths. This contrasts with the movements of nearshore tuna (Yuen 1970, Holland et al. In press) and swordfish (Carey and Robison 1981) which frequently display cyclical diel movements that bring the fish back to their starting points. If Pacific blue marlin have such a pattern in Hawaiian waters, the cycle time for this behavior is longer than any of the tracks so far obtained. At present, the impression is that these animals swim along straight or slightly curving courses as they move through the area.

It is difficult to explain the difference in tagging mortality between this study in which no fish died and the previous one in which three of the five blue marlin died (Yuen et al. 1974). Holts and Bedford (In press) also report that none of their 11 striped marlin died as a result of tagging trauma. Their results, and the results reported here, support the practice of releasing marlin caught on artificial lures by sportfishing techniques, even if the fish are apparently exhausted.

Acknowledgments

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Diversity, Abundance, and Spatial Distribution of Fishes and Crustaceans in the Rocky Subtidal Zone of the Gulf of Maine*

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Shallow subtidal habitats of the Gulf of Maine harbor important populations of decapod crustaceans and a variety of fish species (Bigelow and Schroeder 1953, Cooper et al. 1975, Hacunda 1981). Because of the economic importance of lobsters, considerable work has been done on the biology and autecology of this species along the northwest Atlantic coast (see, for example, Campbell and Stasko 1986, and papers cited therein). Additional attention has been given to the study of lobster ecology since Mann and co-workers suggested in the 1970s that lobsters were "keystone predators" (sensu Paine 1969) in these systems (Mann and Breen 1972, Breen and Mann 1976, but see Miller 1985). There are relatively few published studies dealing with other common predators, such as fish and crabs, inhabiting shallow subtidal habitats of the coast of Maine. With few exceptions, most studies on fishes have dealt primarily with aspects of feeding and reproductive biology of single species (e.g., cunners: Chao 1973, Olla et al. 1975; sculpins: Moore and Moore 1974; wolffish and cod: Keats et al. 1986, 1987). Long-term temporal and spatial changes of demersal fish assemblages along this coast have been analyzed by Tyler (1971) and Hacunda (1981), and more recently, MacDonald et al. (1984) have studied temporal variation of inshore fish assemblages in Passamaquoddy Bay, Canada. To date, however, mobile predator assemblages (including fish and crustacean species) have not been comprehensively studied along the coast of the Gulf of Maine.

Our study first describes the composition of large mobile predators, particularly decapod crustaceans and fishes, occurring in rocky subtidal habitats at Pemaquid Point, Maine, and secondly examines their distribution, diversity, and abundance patterns on spatial (bathymetric) and temporal scales. The information gathered in this study is then analyzed in terms of seasonal impacts of those species in shallow rocky shores and the importance of these environments as nursery areas for these species.

Materials and methods

The study site was a rocky, shallow, sublittoral area off the southwest side of Pemaquid Point, Maine (43°50′N; 69°31′W). This is a wave-exposed area. The substrate down to ~10–12 m (below Mean Low Water Level, MLWL) consists of a sloping, relatively flat ledge. Large rocks and boulders characterize the bottom between ~12–20 m depth. At depths greater than 20 m the substrate is primarily sand with occasional boulders. A detailed description of this study area, including zonation patterns of benthic organisms, is given in Ojeda and Dearborn (1989).

Two methods were used to sample the mobile fauna of this region: gillnets and underwater observations. To determine diversity and abundance of fish species, two 3× 40 m experimental gillnets consisting of four panels (graded in mesh size from 10–20 mm to 60–70 mm) were randomly set in parallel on the bottom, perpendicular to the shore at depths between 5 and 23 m, and about 300 m apart.

Fish were sampled monthly for 2 to 3 days from June 1985 to October 1986, except in July, October, and December of 1985, and January 1986. Gillnets were usually set within the first hour after sunrise and retrived an hour before sunset. All captured fish were fixed in a 5–10% solution of buffered (borax) formalin-seawater mixture, placed in labeled plastic bags, and transported to the laboratory for further analysis. Preserved fish were identified, counted, measured (total length = TL) to the nearest 1.0 mm, and wet weighed to the nearest 1.0 g on a Mettler P1200 balance.

Temporal changes in fish abundance were determined by using a catch-per-unit-effort (CPUE) measurement. This index was calculated as the total number of fish captured

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Table 1

List of fish species found in rocky subtidal habitats at Pemaquid Point, Maine. N = total number of individuals captured in gillnets; % = percent of captures.

	Common name	N	%	Size range (cm TL)
Class Chondrichthyes				
Squalus acanthias Linnaeus	spiny dogfish	42	6.7	87.0–118.0
Raja erinacea Mitchill	little skate	2	0.3	47.0–51.0
Class Osteichthyes				
Alosa sapidissima (Wilson)	American shad	11	1.8	27.5–38.5
Clupea harengus (Linnaeus)	Atlantic herring	2	0.3	6.2–6.4
Osmerus mordax (Mitchill)	smelt	2	0.3	21.7–22.7
Gadus morhua (Linnaeus)	cod	22	3.5	18.7–54.0
Microgadus tomcod (Walbaum)	tomcod	2	0.3	23.6–25.1
Pollachius virens (Linnaeus)	pollock	219	35.21	11.5–30.0
Merluccius bilinearis (Mitchill)	silver hake	4	0.6	15.2–18.2
Centropristis striata (Linnaeus)	black seabass	9	1.4	23.5–26.0
Pomatomus saltatrix (Linnaeus)	bluefish	6	1.0	60.0–86.0
Stenotomus chrysops (Linnaeus)	sculp	3	0.5	20.4–23.3
Tautogolabrus adspersus (Walbaum)	cunner	161	25.8	9.5–32.0
Scomber scombrus Linnaeus	mackerel	47	7.5	27.3–47.2
Pholis gunnelus (Linnaeus)	rock gunnel	*	–	–
Ulvaria subbifurcata (Storer)	radiated shanny	*	–	–
Hemitripterus americanus (Gmelin)	sea raven	22	3.5	23.2–46.0
Myoxocephalus aenaeus (Mitchill)	grubby	2	0.3	9.5–13.2
Myoxocephalus scorpius (Linnaeus)	shorthorn sculpin	26	4.2	20.3–33.0
Myoxocephalus octodecemspinosus (Mitchill)	longhorn sculpin	25	4.0	18.5–43.5
Cyclopterus lumpus Linnaeus	lumpfish	1	0.2	27.0
Limanda ferruginea (Storer)	yellowtail flounder	6	1.0	33.0–36.0
Pseudopleuronectes americanus (Walbaum)	winter flounder	10	1.6	18.5–20.0
Total		624		

* Not caught in nets.

in both nets divided by the total number of sampling hours in each month.

To determine the spatial distribution as well as temporal changes in abundance of fish, lobsters, and crabs, visual underwater censuses of these species were conducted during the day using SCUBA across bathymetric transects. A total of 34 transects were made during June, August, September, and November 1985, and February, April, June, July, September, and October 1986. Each transect extended from 0 to ~23 m below MLWL, 5 m wide and ~60–70 m long, covering an area of ~300–350 m^2. The transects were surveyed in segments covering each 3-m depth interval. Two divers independently searched each of these areas exhaustively (in ~20 minutes), recording the number of crabs, lobsters, and fish species (both mobile and benthic ones). Two night-dive transects were conducted during September 1985 to determine nocturnal activity patterns of mobile predators. Four additional transects were carried out in May 1985 to estimate substrate heterogeneity along the depth gradient. Each transect consisted of a polypropylene line extended over the rocky bottom from 0 to 23 m below MLWL. In each of these transects, at depth intervals of 3 m, we recorded the number of crevices, holes, and burrows (shelters) larger than 5 cm in aperture occurring to a distance of half a meter to the right and to the left of the line.

One-way ANOVA followed by a Student-Newman-Keuls (hereafter SNK) multiple comparison test (Sokal and Rohlf 1969) were employed for the detection of changes in abundance of predators and shelters (substrate heterogeneity) over the temporal and bathymetric gradients studied.

Results

Species composition

A total of 4 species of decapod crustaceans, including 1 lobster species (*Homarus americanus*) and three species of crabs (*Cancer irroratus*, *C. borealis*, and *Carcinus maenas*), and 23 species of fish (624 specimens) were captured or observed from June 1985 to October 1986 (Table 1).

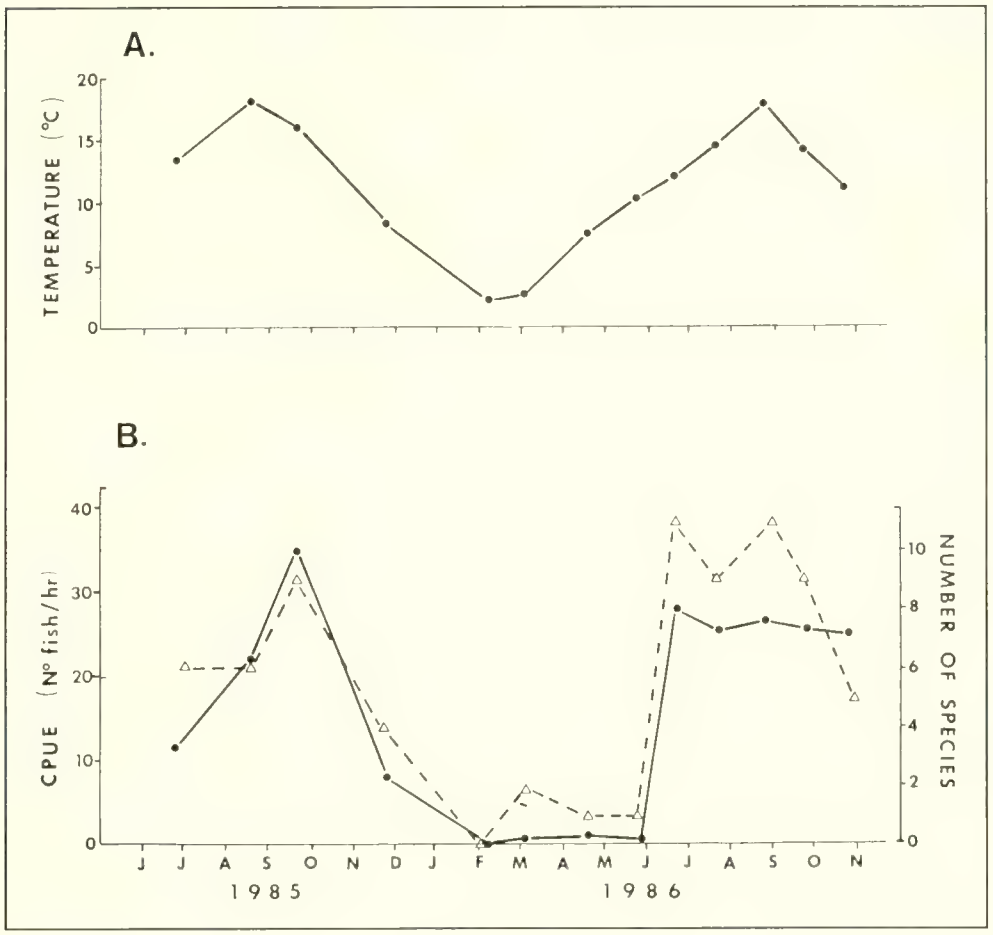

Figure 1
(A) Surface water temperature in Pemaquid Point, Maine, during 1985–86. (B) Temporal variation in the number of species (dashed line) and relative abundance (solid line) of fish captured with experimental gillnets at Pemaquid Point, Maine, during 1985–86. Abundances are expressed as captures per unit effort (CPUE).

The most abundant species were juvenile pollock and cunners (Table 1). Most of these pollock were immature individuals averaging 215 mm TL, which correspond to pollock of about 1 year-old (Bigelow and Schroeder 1953). Six other species were relatively common (represented by more than 2% and less than 10% of the total number of specimens collected: spiny dogfish, cod, mackerel, and sculpins). Most of the cod captured were juveniles averaging 300 mm TL, which correspond to an age of ~2 years (Bigelow and Schroeder 1953). Each of the remaining 13 species (61.9% of the total number of species) were represented by less than 2% of the total number of fish captured (Table 1).

Captures of all three sculpin species, pollock, and cod were significantly greater during the night than during the day (χ^2 test for goodness of fit, $P<0.05$) suggesting that these fish are primarily crepuscular and/or nocturnal predators.

On the other hand, cunners, mackerel, and spiny dogfish were captured almost equally during the day and at night ($P>0.05$). In contrast to mackerel and spiny dogfish, cunners were very rarely observed to be active at night, indicating they are primarily diurnal predators in these environments, as previously shown by Chao (1973), Olla et al. (1975), and Dew (1976).

Temporal patterns

Surface-water temperature of the littoral zone followed a seasonal cycle typical of cold waters of the Gulf of Maine (Fig. 1A), as shown by Tyler (1971) and MacDonald et al. (1984). Maximum values of about 18°C were observed during summer (July–September), and minima of about 1–2°C occurred during winter (February–March). Both the abundance and diversity of fish showed a clear seasonal pattern closely paralleling the seasonal variation of water temperature (Fig. 1B). Fish abundance peaked during summer, reaching values of 30–34 fish/hour, and was lowest (near zero) during winter. Species diversity followed a similar seasonal pattern (Fig. 1B). These results suggest a seasonal migration (inshore–offshore) of most components of this fish assemblage, which appears to be correlated with temperature changes.

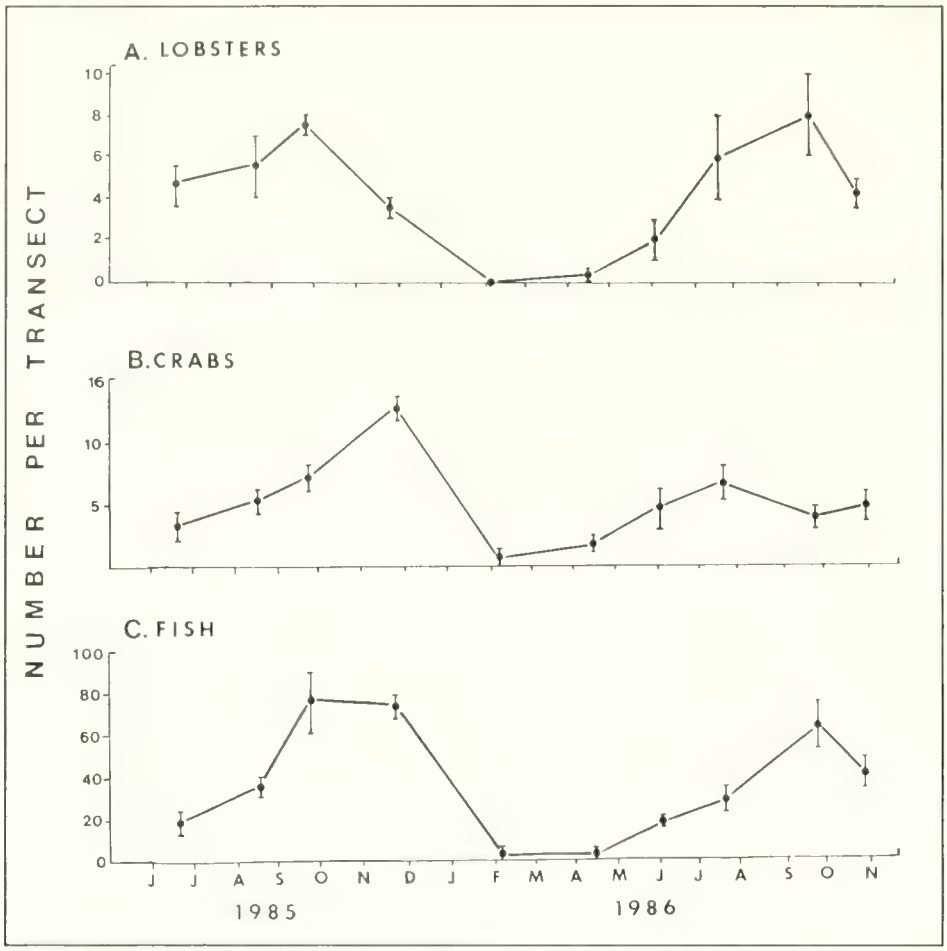

Figure 2
Seasonal variations in the abundance of lobsters (A), crabs (B), and benthic fish (C) along bathymetric underwater transects at Pemaquid Point, Maine. Each vertical bar indicates ±2 SE.

The abundance of major components of the catch—lobsters, crabs, and benthic fishes—also varied seasonally (one-way ANOVA, $P<0.01$ for all species; Fig. 2). Maximum abundances of lobsters occurred in summer (July–September) at densities of 5–8 individuals per transect (~1 adult lobster per 26 m^2) (Fig. 2A). No lobsters were observed in the winter transects (February 1986). The seasonal distribution of lobsters closely follows the seasonal variation in water temperature (compare Figures 1A and 2A). Highest densities of crabs, however, occurred in late fall (November) 1985, with ~14 individuals per transect (~1 adult crab per 12 m^2), and during the summer of 1986, though their densities were markedly lower than those observed in 1985 (~5 crabs per transect or ~1 crab per 33 m^2) (Fig. 2B). Few crabs were observed in winter; of those observed, most remained inactive and semiburied in the sand.

Benthic fish such as cunners, rock gunnels, sculpins, shannys, flounders, and rays were markedly most abundant during fall months, reaching densities of ~75 individuals per transect in 1985 and ~60 in 1986 (Fig. 2C). Their abundance decreased significantly in winter to 2–4 fish per transect, and progressively increased from mid-spring (May–June) until fall as temperature increased. Exhaustive underwater surveys for large predators were carried out in winter (February 1986) with the aid of underwater lights. No cunners or lobsters were observed along these transects despite the special care taken to examine crevices, caves, and spaces underneath boulders and rocks. In addition to a few crabs, three species of fish were commonly observed along these winter transects: rock gunnels, sea ravens, and winter flounders. Rock gunnels were the most abundant fish species, and they were usually observed up to 20 m depth, often associated with clumps of *Modiolus modiolus*. During the rest of the year, this fish species was rarely found at depths greater than 10 m.

This mobile predator assemblage can be divided into distinctive seasonal components. The first is comprised of "summer–fall residents," species consistently present from late spring until late fall, including pollock, cunners, longhorn and shorthorn sculpins, grubbys,

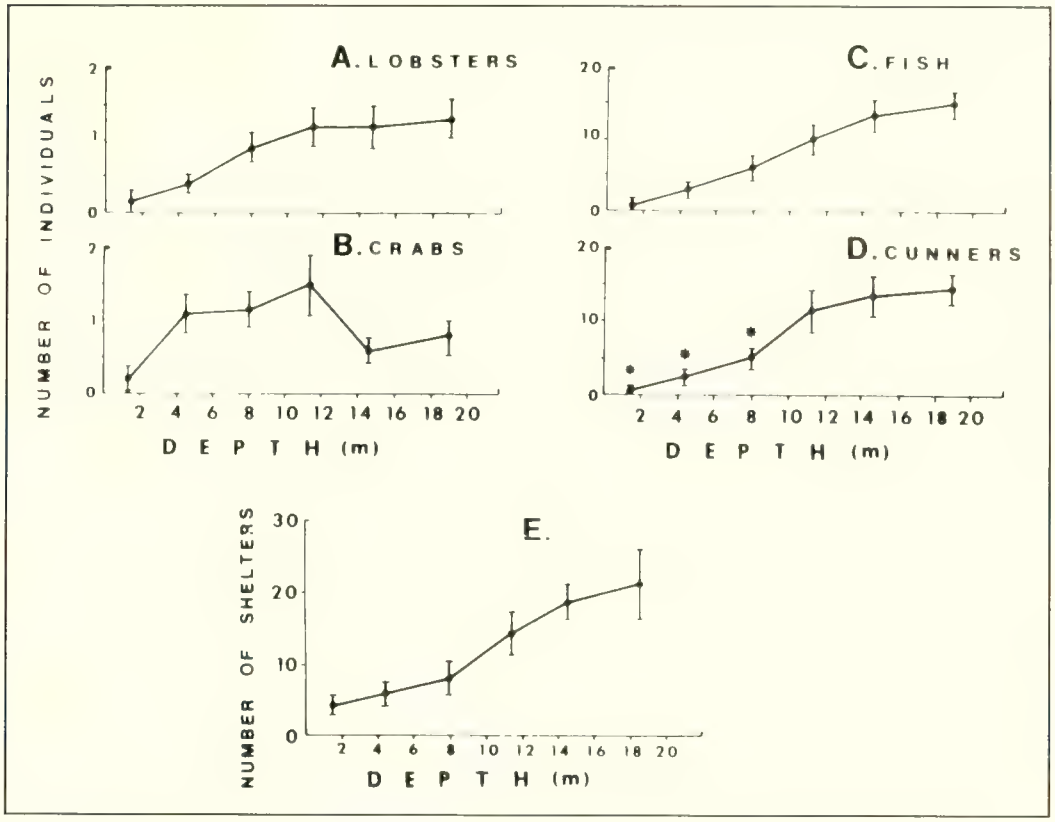

Figure 3
Bathymetric distribution in the abundances of lobsters (A), crabs (B), benthic fish (C), cunners (D), and number of shelters (E) in the underwater transects conducted at Pemaquid Point, Maine. Each vertical bar indicates ±2 SE. Asterisks in D indicate juvenile individuals.

cods, and lobsters and crabs. Lobsters and crabs, however, occurred earlier than these fishes. Crab species are included in this group because their abundance was extremely low during winter, and the few individuals that remained were not active. Summer–fall resident species moved into shallow water or became active (crabs) when the water temperature increased to 8–12°C, generally reaching maximum abundance in midsummer or early fall. The second component was the "regular residents," species captured or observed active at any season, such as sea ravens, rock gunnels, and winter flounders. These species, however, were generally much less abundant than the summer–fall residents (Table 1). The third temporal component of this fauna was the "summer periodicals" (sensu Tyler 1971), and refers to those species that occurred periodically in the samples during summer. The most abundant and conspicuous species in this group were mackerel, spiny dogfish, bluefish, and, less abundantly, black seabass and yellowtail flounder (Table 1). Finally, there was a group of species that occurred at infrequent intervals and in low numbers during this study. Fish species belonging to this group have been called "occasionals" (Tyler 1971) and include shad, little skate, lumpfish, scup, smelt, Atlantic herring, silver hake, and tomcod.

Spatial patterns

The abundances of most groups of mobile predators increased with depth, as did the number of shelters (Fig. 3). The number of adult lobsters significantly increased with depth in the first 8 m, then remained relatively constant thereafter to 19 m depth (one-way ANOVA, $P<0.01$; *a posteriori* SNK test; Fig. 3A). There was no relationship between depth and lobster size, since both large and small individuals were observed at all depths along the transects. Crab species (mostly *Cancer irroratus* and *C. boralis*) showed a somewhat different bathymetric pattern (Fig. 3B). Their abundance markedly increased between 2 and 5 m depth, remained relatively constant at 5–11 m, and decreased at depths greater than 14 m (one-way ANOVA, $P<0.01$, *a posteriori* SNK test). The collective abundance of benthic fishes (e.g., cunners, rock gunnels, radiated shannys, sculpins, and flounders) progressively increased along the bathymetric gradient, reaching highest density at the deeper zone (18–20 m depth; one-way ANOVA, $P<0.01$; *a posteriori* SNK test) (Fig. 3C). A large proportion of these fish, however, were cunners which comprised about 80% of the total number of individuals observed in the transects. Cunners exhibited a distribution pattern similar to the one described for total fish

(one-way ANOVA, $P<0.01$; *a posteriori* SNK test; Fig. 3D). In contrast to adult cunners, juvenile cunners (<5 cm) comprised more than 90% of the total cunners sighted in the first three depth stations (i.e., 2–8 m depth) along the transects.

The number of shelters (a measure of substrate heterogeneity) significantly increased with depth (one-way ANOVA, $P<0.01$; Fig. 3E). This increment is due to the increasing number of large rounded rocks observed at the deeper (10–20 m) transects which create large numbers of interstices (holes) suitable for predators' occurrence.

Discussion

A diverse assemblage of mobile predators inhabits the shallow rocky subtidal zone at Pemaquid Point, Maine. These subtidal habitats are utilized by these species for multiple purposes such as nursery grounds, feeding grounds, shelter, and reproductive activities (Olla et al. 1975, MacDonald et al. 1984, Keats et al. 1987, Ojeda 1987). The occurrence and abundance patterns of these species are, however, markedly seasonal and closely follow the temperature regime typical of northwest Atlantic waters. This suggests that temperature is one of the major abiotic factors affecting the distribution of these predator species on this coast, a finding in agreement with other studies (Tyler 1971; Hacunda 1981; Ennis 1984b; MacDonald et al. 1984; Keats et al. 1986, 1987).

Four temporally distinct components were recognized in this predator assemblage: summer–fall residents, regular residents, summer periodicals, and occasionals. Similarly, Tyler (1971) distinguished four temporal groups in the demersal fish assemblage occurring in Passamaquoddy Bay, New Brunswick, which have also been recognized in other demersal ichthyofaunas of the Gulf of Maine (Hacunda 1981, MacDonald et al. 1984). Three of the four categories of Tyler (1971) were recognized in this study: "regulars," "summer periodicals," and "occasionals." No representatives of Tyler's (1971) fourth category ("winter periodicals"; i.e., species occurring only during winter) were found in this study. This result, however, should be taken cautiously because no samples were taken in midwinter. The most conspicuous and abundant species of mobile predators in this study were summer–fall residents (e.g., cunners, pollock, lobsters, and sculpins), which occurred for most of the warm period in shallow rocky habitats. Summer–fall residents undergo small-scale migrations, moving into deeper, warmer water (>4°C) during winter and returning to shallow subtidal areas in spring. These seasonal movements occur in response to changes in water temperature and probably to physical disturbances such as strong water surges and storms along some exposed coasts. This seasonal migratory behavior represents a behavioral stratety to avoid freezing that involves no physiological adjustment. An alternative strategy involves the elaboration of macromolecules which possess unique antifreeze properties (e.g., glycopeptides in sea raven and winterflounder: Duman and De Vries 1974, Slaughter et al. 1981).

There are conflicting results in the literature concerning winter migration and activity of cunners and lobsters. Several authors have shown that cunners and lobsters do not migrate into deeper waters during winter (Green and Farwell 1971, Cooper et al. 1975, Olla et al. 1975, Dew 1976). However, investigations have shown that cunners (Chao 1973) and lobsters (Ennis 1984b) move to deeper waters in winter as suggested in this study. Recently, Ennis (1984b) showed that small-scale movements of lobsters in Newfoundland were related to increased turbulance due to storms. This is a likely explanation for the absence of lobsters and cunners during winter at Pemaquid Point in this study. As mentioned above, Pemaquid Point is an exposed site (Ojeda 1987). During winter, this area is severely affected by periodic storms and heavy water motion that usually generate strong turbulence over a wide depth range. For organisms that remain in dormant states in shallow waters during winter (such as cunners), water movements may severely restrict their distribution. Most studies documenting the presence of cunners in inshore habitats during winter have been conducted in bays or in other protected areas away from heavy water motion (e.g., Green and Farwell 1971, Olla et al. 1975, Dew 1976). In contrast, documentation of offshore movements of cunners during winter comes from studies conducted on exposed coasts, such as that of Chao (1973). A similar situation seems to occur in lobsters (Ennis 1984b) and probably with crab species which strongly suggests that water movement from turbulence and heavy surge is an important factor, in addition to water temperature, affecting the temporal and spatial distribution of large organisms in shallow subtidal environments of the Gulf of Maine.

Shallow rocky subtidal habitats along the northern New England coast harbor a diverse community of marine organisms providing abundant food resources to seasonal fish residents, occasional migratory fish species, and large crustacean predators (Ojeda 1987). This is so despite the general paucity of kelp beds in this coast, which are an important determinant of the abundance and diversity of nearshore fish and large decapod crustaceans on other temperate coasts (Quast 1968, Moreno and Jara 1984). In addition to acting as feeding grounds, shallow rocky environments also

provide large mobile predators with microhabitats for shelter against predation, and bases for reproductive activities and nursery grounds. Of particular relevance in these environments is the spatial heterogeneity of the bottom. Large rocks and boulders which typically occur at depths greater than 10 m at the study site are important microhabitats for territorial predatory species such as cunners and lobsters (Pottle and Green 1979, Ennis 1984a). The increased number of lobsters and fish (mostly cunners) observed along the bathymetric gradient is probably related to the availability of such microhabitats (see Figure 3). As shown elsewhere (Ojeda and Dearborn 1989), the substrate heterogeneity at Pemaquid Point progressively increases with depth as bottom irregularities such as cracks, crevices, holes, and rocks become more common. In addition to microhabitat availability, the observed bathymetric distribution of large predators may represent an avoidance response by these species to strong water turbulance and wave surge that commonly affect the shallower end of this subtidal zone (especially at low tides).

The occurrence in this study of numerous juvenile pollock and cod provides a good example of the importance of shallow, rocky, subtidal zones as nursery grounds as shown by MacDonald et al. (1984) and Keats et al. (1987). Juvenile pollock were the most abundant species of the nearshore fish assemblage (Table 1). These findings, in addition to feeding data presented elsewhere (Ojeda 1987), suggest that pelagic fish species may play important roles in rocky nearshore benthic communities by affecting the distribution and abundance of their benthic prey. Moreover, the one-way offshore migration exhibited by these species indicates that they may be important linkages in the transfer of energy from nearshore to offshore ecosystems.

Acknowledgments

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A Seasonal Autoregressive Model of the Anchovy *Engraulis encrasicolus* Fishery in the Eastern Mediterranean

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Accurate forecasting is a difficult issue mainly because forecasters are confronted by all sorts of uncertainty (in resource production, budgets, political decisions, etc.) (Hilborn 1987). Although not widely employed, Auto-Regressive Integrated Moving Average (ARIMA) stochastic models (Box and Jenkins 1976) have been successful in describing and forecasting the fishery dynamics of a wide variety of species (lobster: Boudreault et al. 1977, Saila et al. 1979; tuna: Mendelssohn 1981; pilchard: Stergiou 1989a). Although multivariate, deterministic models (e.g., regression models: Ryan 1986, Koslow et al. 1987) are more common in fishery forecasting, these deterministic models often suffer from (1) artificial correlations introduced to the data, (2) residual autocorrelation, (3) high residual variance, and (4) colinearity between the independent variables that may bias the fit (Stergiou 1989b, In press).

In this note, a seasonal autoregressive model is presented that produces forecasts of the monthly purse-seine catches of anchovy *Engraulis encrasicolus* in Greek waters. The anchovy is one of the most important pelagic fish, in terms of biomass, in the Mediteranean Sea. Mean annual anchovy catch in Greek waters during 1982–85 amounted to 12 820 t, representing 17% of the total marine catch (Stergiou 1989b). Of the anchovy catch in Greek waters, 96% is attributed to the purse-seine fishery, accounting for 26% of the total purse-seine catch (Stergiou 1986a, b). Monthly catches of anchovy for January 1964–December 1986 (Fig. 1) (National Statistical Service of Greece 1968–88) show a marked seasonal pattern (Figs. 1, 2) and an increasing trend in the variability of monthly catches for the years following 1980. The latter may indicate that anchovy has suffered recruitment overfishing in recent years (since the late 1970s, purse-seine fishing in Greek waters is anchovy-oriented rather than pilchard-oriented due to the higher price of anchovy [Stergiou 1986b, 1989a, 1990]).

The ARIMA processes (Box and Jenkins 1976, Makridakis et al. 1983) apply to stationary series (time series with no systematic change in mean and variance and free of periodic variations). First- or second-order differencing (nonseasonal and/or seasonal) handles problems of nonstationarity in the mean, and logarithmic (or power) transformation of the raw data handles nonstationary variance. The general form of the ARIMA models,

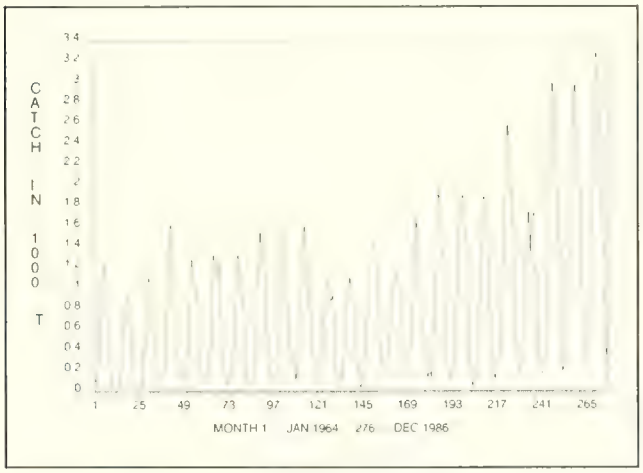

Figure 1
Monthly catches of anchovy in Greek waters, January 1964–December 1986.

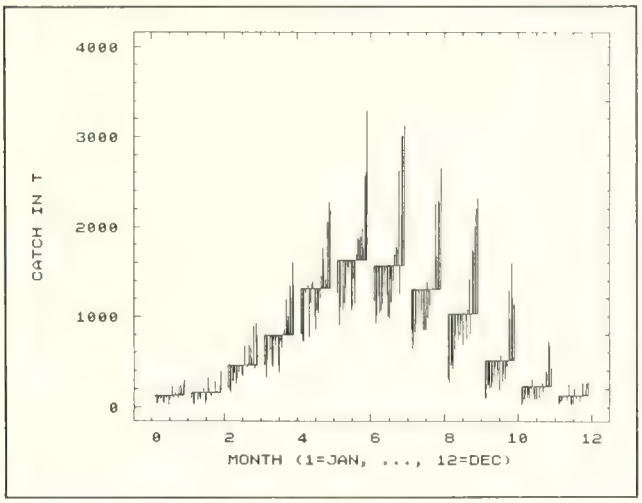

Figure 2
Seasonal subseries plot of monthly catches of anchovy in Greek waters, 1964–86. Horizontal lines represent the average catch of each month. Vertical lines are plotted from the average catch to the actual catch of each year of the 1964–86 period.

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$$\text{ARIMA } (p,d,q)(P,D,Q)^S,$$

can be described by the following equation:

$$(1 - n_1 B^p)(1 - N_1 B^P)$$

$$(1 - B^d)(1 - B^D)X_t = (1 - u_1 B^q)(1 - U_1 B^Q)e_t$$

where X_t = the value at time t, B^p is a backward shift operator that is used as $B^p X_t = X_{t-p}$, n_1, N_1, u_1, and U_1 = arithmetic coefficients, e_t = error term at time t, p = order of autoregressive term (AR term), d = degree of differencing involved to achieve stationarity (I term), q = order of moving average term (MA term), and S = seasonality (number of periods per season); P, D, Q = seasonal terms (corresponding to p,q,d respectively).

Based on the examination of autocorrelation and partial autocorrelation functions (not shown here) of the original logarithmically transformed series, the following model was fitted to the logarithms of the raw data,

$$\text{ARIMA } (1,1,0)(1,1,0)^{12} \text{ (Table 1)},$$

or, after substituting the autoregressive coefficients and expanding the backward shift operator (X_t = logarithm of raw data),

$$X_t = 0.792X_{t-1} - 0.208X_{t-2} + 0.684X_{t-12}$$
$$- 0.862X_{t-13} + 0.138X_{t-14} + 0.336X_{t-24}$$
$$- 0.266X_{t-25} - 0.07X_{t-26} + e_t.$$

The unit of time (t) is one month. The model was estimated using the approximate maximum-likelihood algorithm of McLeod and Sales (1983). Parameters were estimated using backcasting with length of 13.

The examination of the cumulative periodogram of the residuals (not shown here) (Box and Jenkins 1976) indicated that residuals approximated random noise. Actual catches for January 1985–December 1986, not used in the development of the model, and forecasts for those years are plotted in Figure 3. The coefficient of determination (Table 1) was found to be $r^2 = 0.94$ for January 1985–December 1986 (for the untransformed series).

Mean absolute percentage error (MAPE) (Table 1) for January 1985–December 1986 was 20.4%. Except for March and October 1985 and February, October and November 1986, when the absolute percentage error (APE) was higher than 26% (Table 1), monthly catches were predicted reasonably accurately within an APE range of 2–26% (MAPE of the remaining 19 forecasts was 11%) (Table 1).

Table 1

Parameter estimates of the anchovy fishery model. MAPE = mean absolute percentage error, APE = absolute percentage error, r^2 = coefficient of determination.

APE =

$$\frac{\text{Absolute (actual catch at time } t - \text{ forecast at time } t) \ 100}{\text{Actual catch at time } t}$$

MAPE = mean of APE, and

r^2 = 1 – (variance of residuals)/(variance of variable)

Parameter	Estimate	SE	Significance
n_1	−0.208	0.067	$p<0.01$
N_1	−0.336	0.059	$p<0.001$
r^2 for 1985–86		0.94	
Residual mean		0.007	
MAPE 1985		13.3	
MAPE 1986		27.4	
MAPE 1985–86		20.4	
APE>26%			
March 1985		31.5	
October 1985		33.5	
February 1986		47.7	
October 1986		65.9	
November 1986		95.6	
MAPE excluding APE>26		11	

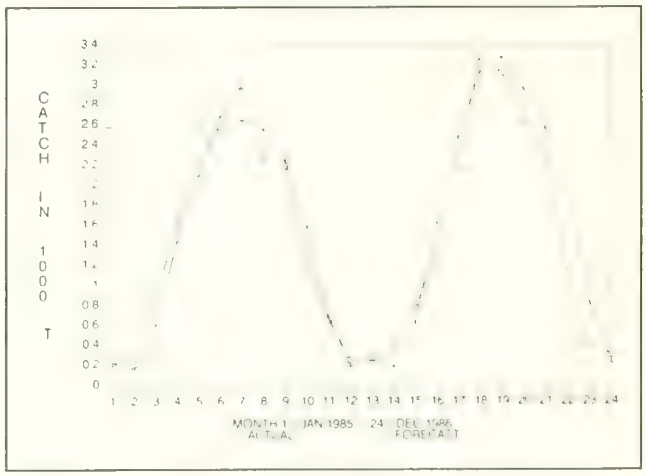

Figure 3

Comparison between actual monthly catches (□) of anchovy in Greek waters during January 1985–December 1986 and the forecasts (+) estimated from the model.

The error in predicting the February–March and October–November catches may be attributed to the highly variable timing of the initiation of the inshore (prespawning migration, which occurs sometime in March) and the offshore migrations (in fall) both of which are expected to be affected greatly by ocean-

ographic conditions. Catches exhibit a marked seasonal pattern (Figs. 1, 2) which is likely related to these seasonal offshore and inshore migrations. Purse-seine fishing activity in Greek waters does not operate in the open sea but is mainly restricted to coastal areas where schools of anchovy migrate on a seasonal basis. The anchovy starts its inshore migration in early spring, but the peak occurs in coastal waters in May–August and schools disperse again during late summer–fall (Fig. 2; Tsimenidis and Caragitsou 1984).

In Greek waters trawling and coastal seining are prohibited from the 1st of June to the 30th of September. As a result, the landings of demersal species (e.g., *Merluccius merluccius*, *Micromesistius poutassou*, *Lophius* sp., *Mullus* sp., *Pagellus* sp.) are low. This combined with the increased demand for fish in summer, drives up fish prices in Greece. In this context, accurate forecasts of the catches of anchovy (and of pelagic fish in general) during June–September are essential for market and industrial planning. APE in June–September was <11.2% in 1985 (mean 7.7%) and <10.6% in 1986 (mean 7.8%).

Strict monitoring and accurate forecasts are essential for pelagic fisheries that are heavily dependent on a single year-class, inasmuch as they are prone to collapse when conditions for recruitment in a particular year are not favorable and fishing is intense (as for anchovy in Greek waters). In this context, accurate forecasts of the annual anchovy catch together with information related to optimal management of anchovy estimated by deterministic fishery-management models, can be used by resource managers for the preseasonal adjustment of anchovy fishing mortality. The model produced reasonable forecasts of the annual 1985 and 1986 catches. Total observed annual catches in 1985 and 1986 were 17 544 t and 18 339 t, respectively, while the model predicted 17 369 t and 20 210 t (APE 1% and 10%, respectively). It must be pointed out, however, that although the model will most likely produce accurate forecasts if the anchovy stock is under equillibrium, it may fail to produce reliable forecasts for years characterized by weak year-classes of anchovy. (In fact there may be a lag of some months between the occurrence of a turning point and its recognition by the model; for a general discussion on turning points and out-of-sample forecasting, see Schlegel 1985.)

The model presented here has also an interesting biological interpretation. The seasonal-difference term of the model indicates the seasonal migratory nature of anchovy in Greek waters. Moreover, climate-plankton-anchovy interactions in the Eastern Mediterranean have been found to involve time lags of 2 to 3 years (Pucher-Petkovic et al. 1971). Yet, a 2–3 year cycle has been identified in the variability of different biotic (zooplankton, phytoplankton, fish) and abiotic (air and sea temperature, salinity and air pressure) components of the Eastern Mediterranean/Black Sea ecosystem (Polli 1955; Regner and Gacic 1974; S. Regner 1982, 1985; D. Regner 1985; Dement'Eva 1987; Petrova-Karadjova and Apostolov 1988). The autoregressive terms (X_{t-24}, X_{t-25}, X_{t-26}) of the model seem to be consistent with these biological/oceanographical observations.

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Tethering as a Technique for Assessing Predation Rates in Different Habitats: An Evaluation using Juvenile Lobsters *Homarus americanus*

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Tethering has been used successfully to assess predation rates of a variety of predator-prey systems in several different habitats. The majority of these experiments have used tethered crabs as prey (Heck and Thoman 1981, Wilson 1985, Wilson et al. 1987, Heck and Wilson 1988, Wilson et. al. 1990, Barshaw and Able In press). Fish have also been tethered in different habitats; however, in these experiments the tethered fish could not act naturally, and therefore the technique only showed the differences in predator encounter rate in different habitats (Shulman 1985, McIvor and Odum 1988). Other organisms are presently being used in tethering experiments including molluscs (R.N. Lipcius and L.S. Marshall, Jr., Coll. William and Mary, Va. Inst. Mar. Sci., Gloucester Pt., VA 23062, unpubl. data) and spiny lobsters (Herrnkind and Butler 1986).

We determined if tethering was an appropriate technique to assess predation on species that burrow (i.e., juvenile lobsters *Homarus americanus*). Lobsters were chosen for this study, in part, because their behavior has been well studied and, therefore, a baseline of "normal" behaviors is available (Botero and Atema 1982, Barshaw and Bryant-Rich 1988).

Lobsters use different methods of constructing burrows in different habitats; therefore we tested three habitats known to be important for early juvenile lobsters: mud, cobble, and *Spartina* peat (Able et al. 1988, Barshaw and Lavalli 1988).

Methods and materials

Six "ant farm" aquaria (10 cm wide, 30 cm long, 45 cm deep) were 2/3 filled with either cohesive mud, cobble of a natural size distribution, or *Spartina* peat substrates (two replicates per substrate type) and provided with running, unfiltered seawater. Early juvenile lobsters (8–14 mm carapace length) were individually tethered to monofilament line using "super glue" to attach it to their carapace. Individual tethered lobsters were placed into half the tanks while similar-sized untethered control lobsters were placed into the remaining tanks.

A discrete reading of each lobster's behavior was recorded every minute for the first 20 minutes, every 5 minutes for the next 35 minutes, and then every hour for 6 hours. A final assessment of each lobster's burrow was made after 24 hours. Therefore, each lobster was observed 33 times over 24 hours in each test. Seven tests were run using all the substrates, with two extra tests run only with mud; thus observations were made on a total of 14 lobsters in cobble, 14 in peat, and 26 in mud. The behaviors observed are described in Table 1.

The behaviors of the tethered and untethered lobsters were compared by calculating the percent of the 33 observations in which the lobsters were engaged in each of the behaviors for each test. Since this experiment was designed only to compare tethered and untethered lobsters, no comparisons were made between different behaviors or between different substrates (comparisons of that nature were studied in Barshaw and Bryant-Rich 1988). The percent of observations was transformed using the arc-sign transformation, and analyzed with a Student's t test. The numbers of the tethered and untethered lobsters that had burrows at the end of the experiment were analyzed for each substrate using 2×2 contingency tables and chi-square tests.

Results

The tethering of juvenile lobsters resulted in substrate-specific differences in behavior and the ability to construct burrows. There were no significant differences between the behavior of tethered and untethered lobsters in the peat or cobble substrates (Fig. 1); in both peat and cobble, all the tethered (7/7) and all the untethered (7/7) lobsters had burrows that they constructed and maintained throughout the experiment.

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Table 1
Description of behaviors of tethered and untethered juvenile *Homarus americanus* observed in this experiment.

Behavior	Description
Rest (RST)	No movement for at least 30 seconds. Grooming was not considered movement and was not recorded separately from RST.
Pleopod fan (PPF)	Movement of the pleopods which caused sediment to be moved; i.e., was being used to build or repair the burrow. In this study PPF which only moved water was not recorded.
Bulldoze (BLD)	Pushing sediment forward with the claws and first walking legs spread apart.
Dig	Loosening sediment by pushing claws into it.
Walk (WLK)	Walking on the sediment; does not include "walking" in the burrow.
Swim	Swimming in the water column.

In the mud substrate, however, the tethered lobsters walked significantly more and bulldozed significantly less than the untethered lobsters (t test, $p<0.05$, Fig. 1). (There was a trend in the tethered lobsters to bulldoze less in all of the substrates). Also, in the mud substrate most tethered lobsters were unable to make or maintain a burrow. Only 7.7% (2/13) of the lobsters had constructed a complete burrow, deep enough to hide the lobster at the end of the 24-hour period. This result was significantly different from the untethered group in which 69.2% (9/13) had constructed burrows by the end of the experiment (chi-square test, $p<0.05$).

Discussion

These observations demonstrate a substrate-specific difference in the effect of tethering on the burrowing behavior of juvenile lobsters. While tethering did not substantially effect the behavior or burrow construction of lobsters in peat or cobble, lobsters tethered in mud spent more time walking, less time bulldozing, and were unable to build and maintain a burrow as well as the untethered lobsters. The tethered lobsters in mud would therefore be more vulnerable to predation than the untethered controls, since being without a burrow has been demonstrated to increase mortality due to predation (Barshaw and Lavalli 1988). Heck and Thoman (1981), Heck and Wilson (1988), and Barshaw and Able (In press) conducted predator-prey experiments using tethered crabs as the prey. *Neopanopi sayi*, *Panopeus herbsti*, *Libinia dubia*, *Ovalipes ocellatus*, and *Callinectes sapidus* were tethered using similar techniques as were used in our study. These investi-

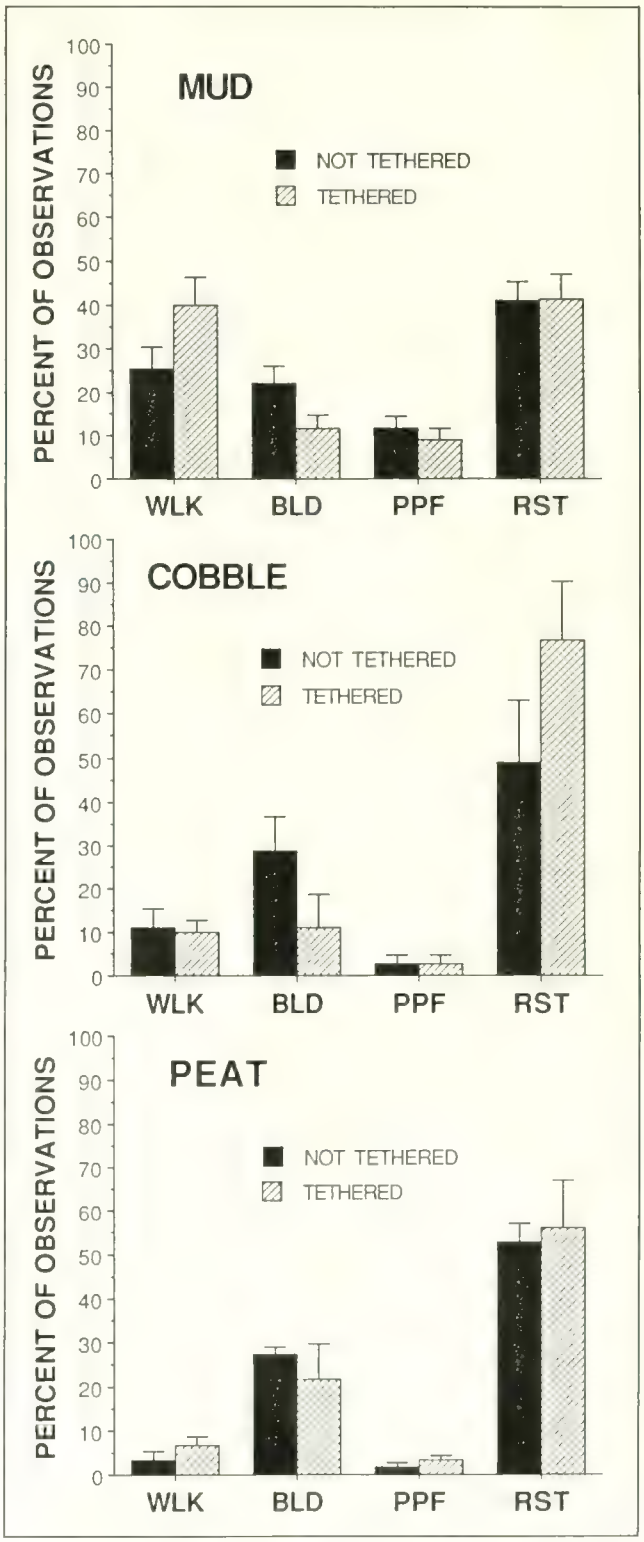

Figure 1
Average percent of the 33 observations in which lobsters were observed doing each behavior in each substrate. WLK = walk, BLD = bulldoze, PPF = pleopod fan, RST = rest.

gators did not observe any differences in the behavior of crabs tethered in different substrates. The differences in tethering effects between these investigations and ours are probably due to the fact that *Homarus americanus* construct burrows in the substrate while the crabs used in the above tethering experiments simply bury themselves directly into the substrate.

The results of this study suggest that tethering to assess predation in different habitats should be evaluated for each new species under consideration because species-specific behavior patterns could create habitat-specific tethering artifacts. In particular, caution should be used when interpreting survival rates of lobsters in mud relative to other substrates. Similar caution should be considered when tethering is used to assess predation in other burrowing forms.

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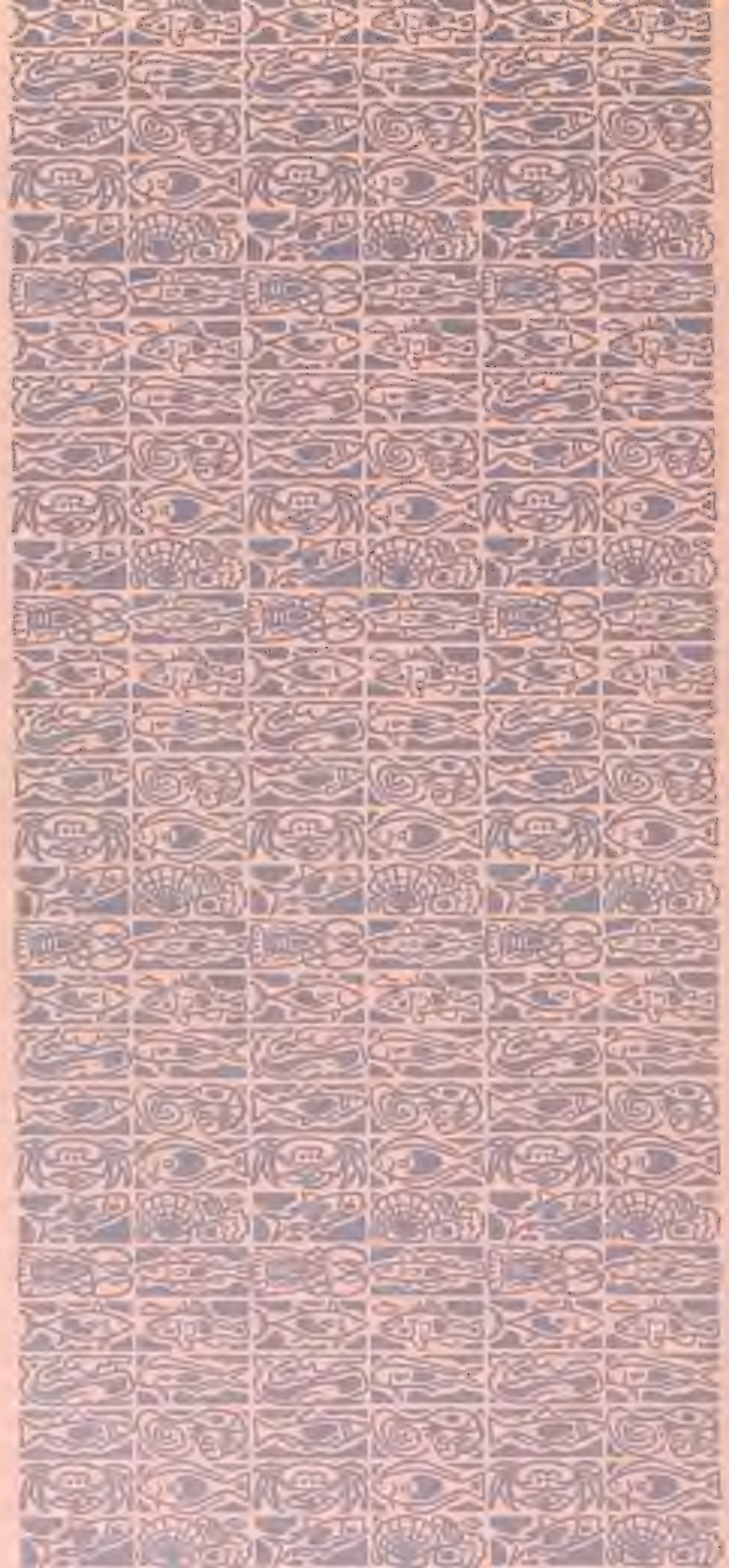

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Abstract.—Winter flounder were acclimated to two temperatures (2° and 7°C) for a period of about 7 weeks prior to spawning. Embryos produced at two acclimation temperatures were incubated through the yolksac stage at three incubation temperatures (4°, 7°, and 10°C). Both adult acclimation temperature and embryo and larval incubation temperature were found to have an effect on larval size and biochemical composition. In many cases the effects of acclimation temperature and incubation temperature were nonadditive. RNA content at first feeding indicated that larvae produced by adults acclimated to low temperature (2°C) were better suited for growth at low temperatures, while larvae produced by adults acclimated to higher temperature (7°C) were better suited for growth at higher temperatures. At first feeding larvae were larger (higher standard length) and in better condition (high protein and RNA content) when incubated at lower temperatures.

Effects of Water Temperature on Size and Biochemical Composition of Winter Flounder *Pseudopleuronectes americanus* at Hatching and Feeding Initiation

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The effects of water temperature on the size and viability of fish eggs and larvae have been the subject of considerable interest. Water temperature is the environmental variable most often linked to recruitment in retrospective empirical analyses of recruitment variability in temperate marine fish (Sissenwine 1984). Yet in most cases causation is not established and the mechanisms involved are poorly understood. Studies of effects of water temperature prior to spawning suggest an inverse relation between water temperature and egg size in several species (Hempel and Blaxter 1967, Cushing 1967, Bagenal 1971, Southward and Demir 1974, Ware 1975, Tanasichuk and Ware 1987). The effects of water temperature during the embryonic period on larval size and yolk conversion efficiency have been examined in a variety of species (Lasker 1962, Sweet and Kinne 1964, Alderdice and Forrester 1968, May 1974, Laurence and Rogers 1976, Linden et al. 1980, Johns et al. 1981, Laurence and Howell 1981, Buckley et al. 1982). While maximum efficiency is generally achieved at intermediate temperatures within the range of thermal tolerance, the exact shape of the relation between temperature and utilization is variable (Heming and Buddington 1988). Blaxter and Hempel (1966) found that the effect of temperature on yolk conversion efficiency was dependent upon egg size in Atlantic herring *Clupea harengus*, cold temperatures favoring small eggs and warm temperatures favoring large eggs. The effects of water temperature have been examined in combination with salinity, oxygen levels, and other environmental variables. None of these studies, with the exception of Tanasichuk and Ware 1987, considered a possible interactive effect of water temperature during gamete maturation with water temperature during the embryonic and larval periods. It is widely known, however, that acclimation temperature mediates many thermal effects, including upper and lower lethal temperatures and metabolic rate (Brett 1970).

This study was undertaken to examine the effects of water temperature during the latter stages of gamete development and during the embryonic and yolksac periods on the size and biochemical composition of winter flounder larvae produced. Standard length, RNA, DNA, and protein content were determined at hatching and first feeding. These indices were chosen because of their relation to fitness, growth, and survival potential of fish larvae. Length

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has been related to swimming speed and the ability to capture prey and avoid preditors (Folkvord and Hunter 1986, Miller et al. 1988). Bulk RNA content is primarily a measure of ribosomal RNA content which is an index of an organism's capacity for synthesis of protein and growth (Bulow 1987). DNA content is an index of cell number and developmental state. Protein, the primary organic constituent in fish larvae, is generally proportional to dry weight (Buckley 1979). Growth of fish larvae is primarily accomplished through protein synthesis and accumulation. Protein is also an important source of reserve energy during larval development (Buckley 1979).

The primary hypothesis tested was that water temperatures, both during gamete maturation and during embryonic and early larval development, and their interaction had an effect on the size and composition of larvae produced. It was reasoned that eggs produced by adults acclimated to low temperatures would be better adapted to low temperatures than eggs produced by adults acclimated to high temperatures. It was expected that the converse was true for eggs produced by adults acclimated to high temperatures. This study originated in part out of an earlier study indicating that winter flounder embryos produced at low temperature exhausted their yolk reserves prior to feeding initiation and appeared poorly suited for growth and survival when incubated and reared at higher temperatures (Buckley 1982). It is part of a larger study of the effects of parental and environmental factors on the size and viability of winter flounder eggs and larvae. The rationale for this larger effort is that given the high fecundity of temperate marine fishes and the high mortality rates during their early life stages, variability at the individual, brood and stock level in size and composition of fish eggs and larvae may play a large part in determining survival during the early life stages and consequently in determining recruitment success.

Methods

Mature winter flounder were caught with an otter trawl on 23 December 1980 in the West Passage of Narragansett Bay in the vicinity of Fox Island at a water temperature of 3.5°C (Table 1). Fish were randomly assigned to two groups (acclimation temperatures). One was held at 2°C, the other at 7°C. Spawning was induced by injections of carp pituitary extract administered as described by Smigielski (1975). Eggs were stripped, fertilized with the sperm of three males held at the same temperature as the spawning female, and treated with diatomaceous earth (Smigielski and Arnold 1972). Embryos from each female were randomly split into three groups of about 1500 each and incubated at 4°, 7°, and 10°C in 38-L black glass aquaria. Eggs and larvae were not incubated at 2°C because of the high mortality observed at this temperature in earlier studies (Laurence 1975, Buckley 1982). Embryos were gradually acclimated to the incubation temperatures at the rate of 1°C per 6 hours. After hatching, larvae were fed live zooplankton collected in the Narragansett Bay area and sieved to select the appropriate size fraction. Plankton densities were maintained at greater than 2 plankters per mL.

Table 1

Experimental design. Three *Pseudopleuronectes americanus* females were spawned at each of two acclimation temperatures (2°, 7°C). Subsamples of about 1500 eggs from each female were incubated in separate containers at each of three temperatures (4°, 7°, 10°C). Triplicate samples of 40 larvae each were taken from each tank for biochemical analysis.

Stage	Temperature		Time
Adults	3.5°C		Capture
	↙	↘	
	Acclimation		
Adults–Gamets	2°C	7°C	48–51 days
	↓	↓	
	Incubation		
Embryos–Larvae	4, 7, 10°C	4, 7, 10°C	13–29 days

Groups of 10 larvae were examined daily, between 0800 and 1100 hours, under a dissecting microscope to establish the day of completion of yolksac absorption and first feeding. Larvae were judged to have completed yolksac absorption when 5 out of 10 larvae had no visible yolk. Larvae were judged to have initiated feeding when 5 out of 10 larvae examined had food visible in their gut. At hatching and first feeding 10 larvae from each group (one unique combination of acclimation and incubation temperatures for each female) were measured for standard length with a filar micrometer in a dissecting microscope. Yolk volume was estimated using the equation for a prolate spheroid:

$$V = (\pi/6)\, LH^2$$

where L is the length and H is the height of the yolksac (Laurence 1973). Triplicate groups of 40 larvae each were sampled at the same times for biochemical analysis. Larvae were homogenized in 2.0 mL of ice-cold distilled water using an all-glass tissue grinder. Subsamples of 1.4 and 0.1 mL of homogenate were used for analysis of nucleic acids and protein, respectively, as outlined in Buckley (1979). Nucleic acids were determined using a modification of the Schmidt-Thannhauser method. A modification of the Lowry method was used for determination of protein. Coefficients of varia-

Table 2

Size and number of injections for individual *Pseudopleuronectes americanus* females, and percent fertility and hatch of their offspring.

Acclimation T (°C)	Tag number	Length (mm)	Weight (g)	No. injections	Fertility (%)	Incubation T (°C)	Hatch (%)	Age at hatch (d)	Age at first feeding (d)
2	335	280	290	4	98	4	85	20	9
						7	80	11	7
						10	72	7	2
2	217	301	389	4	75	4	85	17	7
						7	80	10	7
						10	70	8	5
2	218	290	315	3	96	4	85	16	7
						7	80	10	7
						10	70	7	5
7	857	245	345	2	96	4	85	15	8
						7	80	10	6
						10	70	7	4
7	067	303	373	4	98	4	80	14	11
						7	70	10	6
						10	70	7	4
7	276	357	627	3	98	4	80	14	11
						7	80	7	6
						10	80	7	6

tion (sample standard deviation as a percent of the mean) for replicate analyses on portions of a fresh or frozen homogenate run within one week of preparation were 3% for RNA, 8% for DNA, and 5% for protein.

Data analysis was done using SAS System Software for personal computers (SAS 1985). The GLM procedure was used for analysis of variance because of the unbalanced design. Differences among main effect means were tested for significance using Tukey's studentized range test.

Results

Between 48 and 51 days after capture, three females were spawned at each acclimation temperature after receiving between two and four hormone injections (Table 2). There was no significant difference in either the number of injections administered or the length of female parents between acclimation temperature groups (analysis of variance, $P \leq 0.05$). Spawning females ranged in length from 245 to 357 mm with a mean of 296 mm. Based on length-at-age data for winter flounder from the Niantic River, CT (Northeast Utilities 1987), this corresponds to a range in age of 3–6 years. Fertilization rate was high, ranging from 75 to 98% with a mean of 94%. Acclimation temperature or the number of hormone injections had no significant effect on the fertilization rate ($P \leq 0.05$). Percent hatch ranged from 70 to 85% with a mean of 78%. Hatch rates were significantly higher at the lower incubation temperatures but unaffected by acclimation temperature of the parents ($P \leq 0.05$).

At all combinations of acclimation (prespawning) and incubation (postspawning) temperature, completion of yolksac absorption occurred within one day of first feeding. Age at hatch and age at first feeding were inversely related to incubation temperature. Spawning temperature had an effect on age at hatch but not on age at first feeding. No interactive effect of adult acclimation temperature and embryo incubation temperature was observed on the rate of these developmental processes ($P \leq 0.05$).

The mean standard length and chemical content of larvae at hatching and first feeding are given in Tables 3 and 4. Standard length and DNA content generally increased over this period (Fig. 1). The decrease in protein content between hatching and first feeding indicates a net catabolism of protein during the period.

The effects of selected factors on the size and chemical content of larvae at hatching and at first feeding were evaluated using analysis of variance (Table 5). In SAS notation, the general form of the model used was:

$$Y = A\ B\ C(A)\ A*B$$

where Y is the dependent variable and A, B, and C

Table 3

Length, yolksac volume, and chemical content of *Pseudopleuronectes americanus* larvae at hatching. Values are the estimated means along with the standard deviation. For standard length and yolksac volume, $N = 30$ (10 larvae from each of 3 females). For RNA, DNA, and protein content, $N = 9$ (3 pools of 40 larvae each from 3 females). Percents in brackets are coefficients of variation of the grand mean. Where the interaction between adult spawning temperature and embryo incubation temperature was not significant, main-effects means were calculated and Tukey's studentized range test applied to these values. Where the temperature interaction factor was significant, simple main effects were tested. Values in a row with a superscrip letter in common or bracketed values in a column are not significantly different ($P \leq 0.05$).

Spawning temperature (°C)	Incubation temperature (°C) 4	7	10	$\bar{x}$
		Standard length (mm)		
2	[3.61 ± 0.15[a]	[3.45 ± 0.17[b]	3.40 ± 0.14[b]	
7	[3.33 ± 0.16[a]	3.46 ± 0.09[b]	–	
$\bar{x}$				3.45 ± 0.18 (6.1%)
		Yolksac volume (mm^3)		
2	0.08 ± 0.04	0.05 ± 0.02	0.05 ± 0.02	0.06[a]
7	0.08 ± 0.04	0.05 ± 0.01	–	0.07[a]
$\bar{x}$	0.08[a]	0.05[b]	0.05[b]	0.06 ± 0.03 (50%)
		RNA content (μg/larva)		
2	1.32 + 0.16	1.18 ± 0.20	1.17 ± 0.09	1.22[a]
7	1.27 ± 0.13	1.13 ± 0.08	1.05 + 0.08	1.16[b]
$\bar{x}$	1.30[a]	1.16[b]	1.11[b]	1.19 ± 0.16 (13.1%)
		DNA content (Mg/larva)		
2	0.34 ± 0.06[a]	[0.2820.04[b]	[0.36 ± 0.04[a]	
7	0.33 ± 0.05[b]	[0.39 ± 0.04[a]	[0.33 ± 0.03[b]	
$\bar{x}$				0.34 ± 0.06 (16.7%)
		Protein content (μg/larva)		
2	17.3 ± 2.4	15.7 ± 4.2	15.8 + 2.7	16.2[a]
7	15.2 ± 2.2	–	15.6 ± 1.7	15.3[a]
$\bar{x}$	16.1[a]	15.7[a]	15.7[a]	15.9 ± 2.8 (17.5%)

Table 4

Length and chemical content of *Pseudopleuronectes americanus* larvae at first feeding. Values and statistics are as given for Table 3.

Spawning temperature (°C)	Incubation temperature (°C) 4	7	10	$\bar{x}$
		Standard length (mm)		
2	4.40 + 0.15[a]	4.18 ± 0.30[b]	[3.96 ± 0.15[c]	4.21[a]
7	4.35 ± 0.09[a]	4.14 ± 0.19[b]	[4.05 ± 0.14[b]	4.19[a]
$\bar{x}$				4.20 ± 0.25 (5.9%)
		RNA content (μg/larva)		
2	[1.30 ± 0.13[a]	[1.21 ± 0.15[a]	[0.89 ± 0.01[b]	
7	[1.17 ± 0.12[a]	[1.01 ± 0.08[b]	[1.21 ± 0.15[a]	
$\bar{x}$				1.15 ± 0.18 (15.2%)
		DNA content (μg/larva)		
2	0.41 + 0.06	0.35 ± 0.07	0.38 ± 0.02	0.38[a]
7	0.37 ± 0.03	0.43 ± 0.06	0.38 ± 0.05	0.39[a]
$\bar{x}$	0.39[a]	0.39[a]	0.38[a]	0.39 ± 0.05 (13.7%)
		Protein content (μg/larva)		
2	13.3 ± 1.6[a]	[12.0 ± 1.8[a,b]	11.0 ± 2.0[b]	
7	13.1 ± 1.0[a]	[13.4 ± 0.9[a]	11.1 + 1.2[b]	
$\bar{x}$				12.8 ± 1.6 (12.5%)

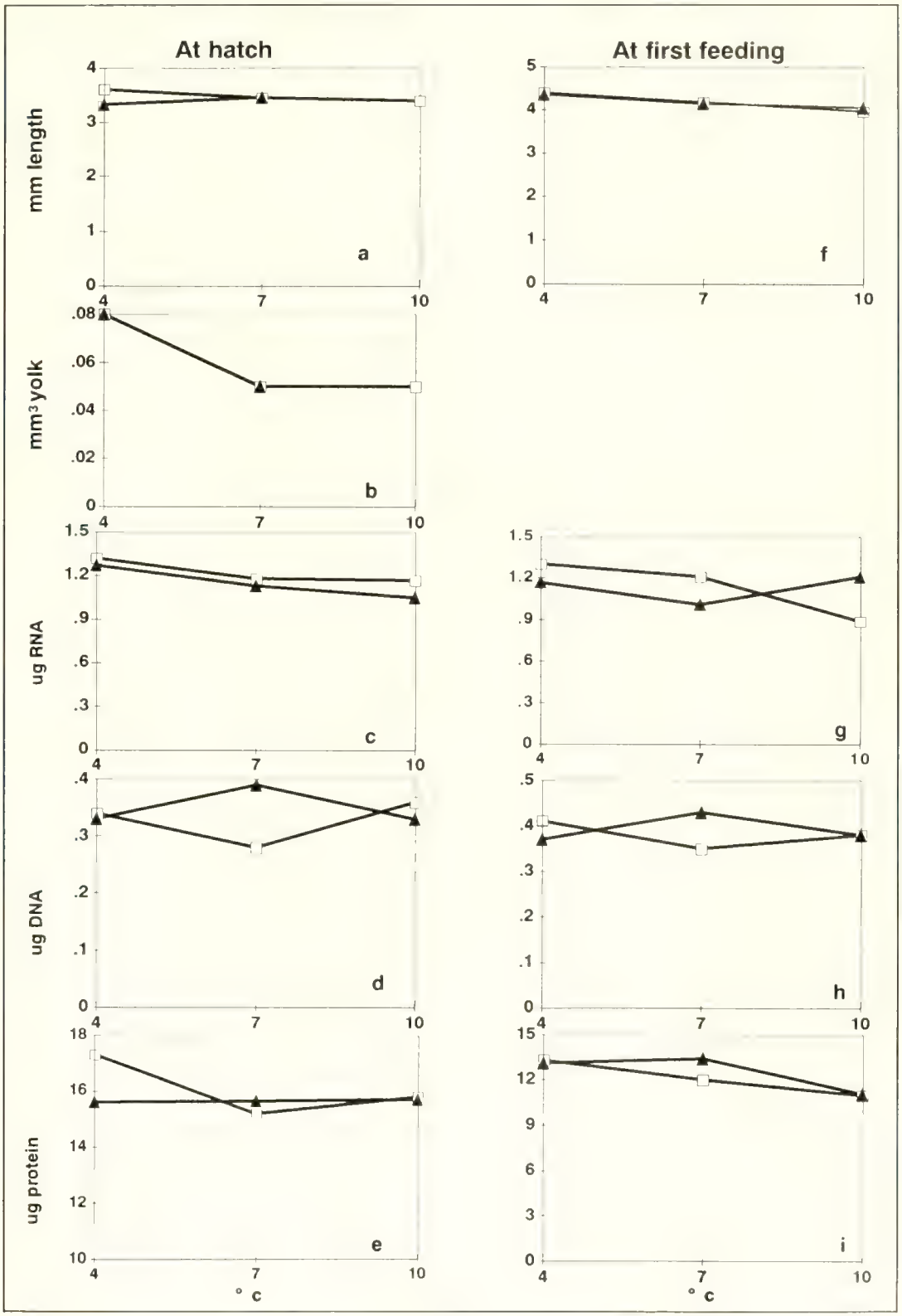

Figure 1

Standard length, yolk volume, and biochemical composition of *Pseudopleuronectes americanus* larvae at hatching and first feeding. □ Tsp = 2°C; ▲ Tsp = 7°C.

Table 5

Analysis of variance for factors affecting size and chemical content of *Pseudopleuronectes americanus* larvae at hatch and first feeding. Tsp = adult acclimation and spawning temperature; Tinc = embryo and larval incubation temperature; T × T = temperature interaction; Block = female tag number. $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$. Where the temperature interaction is significant, F values for Tsp and Tinc are not given.

		Tsp	Tinc	T × T	Block	Total
At Hatch						
Larval length (mm)	df	1	2	2	4	139
	F value			25.17***	13.66***	
Yolk volume (mm^3)	df	1	2	2	4	139
	F value	0.00	12.26***	0.05	2.40*	
RNA (μg/mg)	df	1	2	2	4	49
	F value	4.68*	15.94***	0.18	10.16***	
DNA (μg/mg)	df	1	2	2	4	49
	F value			24.15***	8.41***	
Protein (μg/mg)	df	1	2	1	4	36
	F value	0.00	1.11	0.01	15.59***	
At First Feeding						
Larval length (mm)	df	1	2	2	2	169
	F value			5.07**	8.08***	
RNA (μg/mg)	df	1	2	2	4	41
	F value			40.78***	12.29***	
DNA (μg/mg)	df	1	2	2	4	39
	F value	0.27	1.38	3.13	1.90	
Protein (μg/mg)	df	1	2	2	4	34
	F value			6.32**	11.93***	

are independent class variables (SAS Institute 1985). A is the acclimation and spawning temperature (Tsp); B is the embryo and larval incubation temperature (Tinc); C is the block effect or individual female tag number (Block). This maternal factor is nested within the acclimation temperature and represents the variability among individual spawning females. This factor was added to the model to block out fish-to-fish variability. It was significant for all dependent variables tested (Table 5). $A*B$ is the interaction of acclimation and incubation temperatures.

Significant interactions between spawning and incubation temperature were observed at hatch for length and DNA content, and at first feeding for length, RNA, and protein content. In these cases, where the effects of spawning temperature and incubation temperature were nonadditive, simple main effects were tested at each spawning and incubation temperature using Tukey's studentized range test. Where no temperature interaction was observed (yolk volume, RNA, and protein content at hatch, and DNA content at first feeding) main-effects means were calculated and differences among main-effects means were tested for significance using Tukey's studentized range test.

At hatching, standard length showed a significant temperature interaction (Table 5). At a spawning temperature of 2°C, standard length decreased with increasing incubation temperature (Table 3). At a spawning temperature of 7°C, standard length was higher at an incubation temperature of 7°C than at 4°C. Yolk volume showed no significant temperature interaction, was unaffected by spawning temperature, and was highest at the lowest incubation temperature of 4°C. RNA content at hatch showed no significant temperature interaction and decreased with both increasing spawning and incubation temperature. DNA content at hatch showed a significant temperature interaction. At a spawning temperature of 2°C, DNA content was lowest at the intermediate incubation temperature (7°C). At a spawning temperature of 7°C, DNA content was highest at this intermediate incubation temperature. Protein content at hatch showed no temperature interaction and was unaffected by either spawning or incubation temperature.

At first feeding, standard length showed a significant temperature interaction. At both spawning temperatures (2° and 7°C) standard length decreased with increasing incubation temperature (Table 4). RNA content at first feeding showed a significant temperature interaction. At a spawning temperature of 2°C, RNA content was lowest at the highest incubation temperature (10°C). At a spawning temperature of 7°C, RNA

content was lowest at the intermediate incubation temperature (7°C). DNA content at first feeding showed no significant temperature interaction and was unaffected by either spawning or incubation temperature. Protein content at first feeding showed a significant temperature interaction. At both spawning temperatures, protein content decreased with increasing incubation temperature.

Discussion

Winter flounder spawn and embryos survive over a wide range of temperatures. In the laboratory, Williams (1975) observed survival of embryos between −1.8° and 15°C. Rogers (1976) reported survival between 3° and 14°C. While 2°C is close to the temperature of maximum egg production, winter flounder larvae require water temperatures above 2°C for survival to metamorphosis (Laurence 1975, Buckley et al. 1982). Spawned through the late winter and early spring, winter flounder embryos and larvae generally experience gradually increasing water temperatures. In shallow estuaries and bays, however, embryos and larvae may be subjected to large fluctuations in salinity and water temperature over relatively short periods of time, or to prolonged periods of abnormal warming or cooling. The effects of such changes in water temperature on survival and growth of the early-life stages of winter flounder are largely unknown.

Inverse relations between water temperature (during late winter and early spring) and indices of recruitment have been reported for winter flounder (Jeffries and Johnson 1974, Jeffries and Terceiro 1985, Northeast Utilities 1988). The shape of larval abundance curves, a parameter affected by water temperature, has also been related to recruitment; cold years with broad shallow abundance curves produce good year-classes (Northeast Utilities 1988).

The size and chemical composition of larvae at initiation of feeding provide useful criteria for evaluation of these temperature effects, and may provide insight into causal mechanisms. Feeding initiation is the end point of the period of reliance on endogenous energy reserves that commences at ovulation. Increased larval size confers increased potential for survival, since larger larvae are better able to avoid size-dependent predation, capture food, and survive periods of starvation (Blaxter and Hempel 1966, Rosenberg and Haugen 1982, Bailey and Battey 1984, Knutsen and Tilseth 1985). DNA content is an index of cell number and RNA content an index of the capacity for protein synthesis and hence growth (Bulow 1987). Buckley et al. (In prep.) demonstrated direct relations between size and RNA content of yolksac winter flounder larvae and survival for the first month of life in the laboratory. Size of larvae at first feeding is dependent upon egg size at spawning and the efficiency of production of larval tissue (yolk-conversion efficiency).

Based on observations of the timing of yolk absorbtion and first feeding, and the size and composition of winter larvae produced by a single female spawned at 2°C, Buckley (1982) speculated that eggs spawned at low temperatures (2°) may be poorly suited for growth and survival at high temperatures (10°C) within the range of tolerance of winter flounder. The present factorial study of six females spawned at low (2°C) and high (7°C) temperatures confirmed and extended these earlier findings. However, unlike the earlier study, first feeding occurred within one day of completion of yolk absorbtion at all combinations of adult acclimation (prespawning) and incubation temperature (Table 2). The present study, with the spawn from six winter flounders, demonstrated the importance of variability at the level of individual females in determining size and composition of winter flounder larvae (Tables 3 and 4). Adult acclimation (prespawning) temperature was important alone or in combination with embryo incubation temperature in determining length and RNA and DNA content at hatch, and in determining length and RNA and protein content at first feeding (Table 5). Embryo incubation temperature was important alone or in combination with adult acclimation temperature in determining larval size, yolksac volume, RNA and DNA content at hatch, and in determining length and RNA and protein content at first feeding. At first feeding, size and chemical content of eggs spawned by adults acclimated to 2°C were maximized at the lowest incubation temperature (4°C). Eggs spawned at 7°C produced the longest first-feeding larvae at 4°C, while DNA and protein content were highest at the intermediate incubation temperature (7°C) and RNA content was highest at the warmest incubation temperature (10°C). The largest larvae, whether measured by length or chemical content, were produced at the lowest combination of acclimation and rearing temperatures. RNA content, which is critical to protein synthesis and growth, was highest at first feeding in larvae incubated at 4°C for eggs produced at 2°C, and at 10°C for eggs produced at 7°C. RNA content was lowest in first-feeding larvae produced from eggs spawned at 2°C and incubated at 10°C. This group represented the largest difference between spawning and incubation temperature.

Hempel and Blaxter (1967) reported differences in fecundity and egg size between Atlantic herring stocks spawning at different temperatures. Stocks spawning at colder temperatures produced fewer but larger eggs. Tanasichuk and Ware (1987) working with Pacific herring found that both size-specific fecundity and egg

size, but not size-specific ovary weight, were related to seawater temperature 60–90 days before spawning. Again, fecundity increased with increasing temperature while egg size decreased.

Results from this study demonstrate that water temperatures during the latter stages of gamete maturation (48–51 days prior to spawning) and during embryo and larval development affect the size and composition of winter flounder larvae produced. Further, the interaction between acclimation temperature of adults and incubation temperature of embryos and larvae also appears to have a strong effect on size and composition of larvae. While the number of oocytes entering vitellogenesis is probably determined earlier in the reproductive cycle (Brown 1957, Dunn 1970, Tyler and Dunn 1976, Burton and Idler 1984), several important functions occur during the latter stages of gamete development, including further deposition of yolk and final meiotic division.

Our data on size and chemical composition of winter flounder at hatching and first feeding suggest a more complex relation between water temperature and larval size than observed between water temperature and egg size. These data may help explain some of the variability observed in the relation between yolk-conversion efficiency or maximum larval size and incubation temperature (Sweet and Kinne 1964, Alderdice and Forrester 1968, Laurence and Rogers 1976, Linden et al. 1980, Johns et al. 1981, Laurence and Howell 1981, Buckley 1982). Our data suggest that larval size and composition at hatch and first feeding are dependent not only upon incubation temperature but also upon water temperature during the final stages of gamete maturation and upon the interaction of water temperature during these two time-periods. This implies that the contents of the egg are modified in some way in response to water temperature prior to spawning. Most likely, this temperature response goes beyond simply producing a larger or smaller egg with components in the same proportion. The ratio of major organic components including protein, lipids, carbohydrates, and nucleic acids may be altered in response to temperature. More subtle, but possibly more significant, changes in the composition of the developing oocyte in response to water temperature may include alterations in the content, composition, activity, or stability of enzymes, hormones, maternal messenger RNA, and stable RNA (tRNA and rRNA). Any conclusions about the efficiency of yolk utilization at different incubation temperatures should take into account the thermal history of the spawning adults.

Winter flounder reproductive strategy has most likely evolved to exploit the dramatic increase in water temperature during the spring in the shallow estuaries along the northwest margin of the Atlantic Ocean. Between spawning and metamorphosis, a period of about 2 months in winter flounder, water temperatures warm an average 10°C (from ~2° to 12°C) affecting not only the abundance and composition of predators and prey but also the rates of metabolic processes (Laurence 1975, 1977). This maximizes size and condition of first-feeding larvae at low temperatures (Table 4), allows relatively long resistance to starvation at intermediate temperatures, and facilitates rapid larval and postlarval growth at higher temperatures (Buckley 1982). Mortality of late embryos and larvae at cold temperatures (≤2°C) (Laurence 1975, Buckley 1982) indicates that good survival of winter flounder is dependent upon the expected spring warming. While gametogenesis and embryo and larval development show a wide range of temperature tolerance in winter flounder, these processes appear to have been optimized for cold winter temperatures followed by gradual spring warming. Our data suggest that cold winters followed by gradual spring warming favor good survival and recruitment of winter flounder by facilitating production of the largest larvae at first feeding (high standard length and DNA content) in the best condition (high RNA and protein content). These data may explain in part the observed correlation between cold years and strong year-classes (Jeffries and Johnson 1977, Jeffries and Terceiro 1985, Northeast Utilities 1988).

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Abstract.–This study represents an attempt to distinguish between normal seasonal variations and pollutant-related changes in the blood chemistry of the windowpane flounder *Scophthalmus aquosus*. Three stations in Long Island Sound, USA, were chosen to provide a pollutant gradient. Windowpane flounder were collected from the three stations monthly, when possible, over a period of three years. Seasonal variations were noted in hematocrit, plasma osmolality, sodium, potassium, and calcium. Station-related differences were demonstrated in osmolality, hematocrit, and hemoglobin. The same species was subjected to 60-day laboratory exposures to mercury, cadmium, or copper. Neither copper nor cadmium produced a significant difference in any variable measured. Following exposure to mercury, there were significant differences between controls and exposed animals in plasma sodium and calcium.

Blood Chemistry of the Windowpane Flounder *Scophthalmus aquosus* in Long Island Sound: Geographical, Seasonal, and Experimental Variations

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The geographical situation of Long Island Sound presents unique questions on the distribution of anthropogenic pollutants and the effects of such pollutants on the resident animal population. The western end of the Sound is heavily populated and industrialized. Much of the bottom in the western portions of the Sound consists of fine-grained sediments, with a potential for adsorbing and retaining contaminants (Hunt 1979, Reid et al. 1979). Tidal flushing is limited in the far western end of the Sound; it has been reported that exchange with the East River adds 15 m^3/second of effluent to western Long Island Sound (Bowman 1976).

In contrast, the more eastern portions of the Sound are open to considerable tidal flushing and are bordered by less populated and less industrialized areas. There is a decrease in fine-grained sediments from west to east with a concomitant decrease in the capacity of the sediment to retain contaminants (Hunt 1979, Reid et al. 1979). The physical and geographical differences are reflected in an increase from east to west in sediment levels of heavy metals (Greig et al. 1977, Hunt 1979, NOAA 1988), PCBs (Chytalo 1979, NOAA 1988), and PAHs (NOAA 1988).

The present study is an attempt to assess the effects on a local species of the contaminant levels found in Long Island Sound. Stations were selected on the basis of providing a pollutant gradient and of being located within an area that could be sampled on a day-trip basis, thereby expediting monthly sampling (Fig. 1). Station 1 was off Roanoke Point, New York (lat. 40°58′50″N, long. 72°45′00″W), near the eastern end of the central basin. Reid et al. (1979) reported that this station had less than 5% fine-grained sediments. Greig et al. (1977) reported a sediment cadmium concentration of 1.1 mg/kg dry weight, a copper concentration of 4.0 mg/kg, and a lead concentration of <6.0 mg/kg. Station 2 was off Milford, Connecticut (lat. 40°09′01″N, long. 73°00′00″W), near the western end of the central basin. Reid et al. (1979) reported that this station had a fine-grained sediment level between 5 and 50%. Greig et al. (1977) reported sediment cadmium and mercury levels below detectable limits, a copper concentration of 43.3 mg/kg, and a lead concentration of 19.0 mg/kg. Station 3, Hempstead Harbor, New York (lat. 40°53′50″N, long. 73°49′90″W) is in the western end of Long Island Sound. Reid et al. (1979) reported a fine-grained sediment content of >50%. Greig et al. (1977) reported a cadmium concentration of 1.4 mg/kg, a copper concentration of 175.0 mg/kg, a mercury concentration of 0.7 mg/kg, and a lead concentration of 110.0 mg/kg in the sediment. NOAA (1988) reported a total PCB concentration of 255.5 μg/kg and a total PAH concen-

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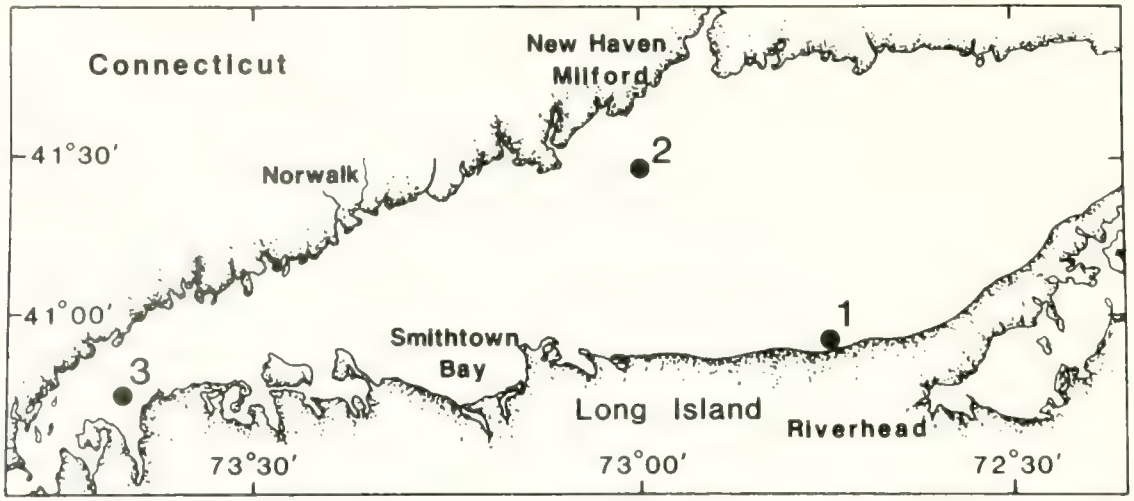

Figure 1

Long Island Sound stations sampled for *Scophthalmus aquosus*: Station 1, off Shoreham, NY, 5.5 m; Station 2, off Milford, CT, 15.2 m; Station 3, Hempstead Harbor, NY, 10.7 m.

tration of 5366 μg/kg in the sediments of Hempstead Harbor.

The windowpane flounder *Scophthalmus aquosus* was chosen as a test animal because it is one of the few species available in the Long Island Sound area throughout the year. The possibility of some movement between stations is a consideration in this type of study. However, Moore (1947) reported on the basis of tagging studies that, although individuals have been shown to move over large distances, no seasonal migration of windowpane flounder is indicated and that this species is relatively stationary.

This study utilized blood chemistry as an indication of stress in the fish. Several investigators have suggested that the study of blood may ultimately be as useful in assessing the health of fish as it is in diagnosing human health (Blaxhall and Daisley 1973, Hickey 1976). Fish blood chemistry has not received the same critical study as has human (Wedemeyer and Yasutake 1977). A given species of fish in its normal habitat is likely to be subjected to a wide range of natural conditions, any of which may be reflected in its blood chemistry. Johansson-Sjöbeck et al. (1975) noted that hematocrit increased and hemoglobin decreased in eels subjected to starvation, both returning to control levels within 164 days. DeWilde and Houston (1967) reported an increase in hematocrit and hemoglobin with an increase in acclimation temperature in rainbow trout; the degree of response depended on season. Effects of heavy-metal exposure on fish blood have been demonstrated (Christensen et al. 1972; Calabrese et al. 1975; Dawson 1979, 1982). Within the same species, freshwater-adapted fish often exhibit blood chemistry which is different from that of fish adapted to seawater (Courtois 1976). Snieszko (1960) emphasized the need to consider two sets of standards in using hemotological methods in hatcheries: one general standard for the species, and a second standard that determines a normal value for the parameter at a particular hatchery.

Although the objective of the present study was to obtain information on pollutant-related stress, it was necessary to consider seasonal changes as well in order to distinguish between the effects of pollutants and those that represent a normal response to changing natural conditions. Although seasonal changes in fish blood have received little attention in the literature, such changes have been documented in the winter flounder (Bridges et al. 1976), the striped bass (Lochmiller et al. 1989) and the rainbow trout (DeWilde and Houston 1967). In addition, the values for hematological measurements vary from species to species, but few species have received sufficient study to allow a realistic estimate of their normal ranges under a reasonable variety of conditions.

The field study described here was supplemented by a series of three laboratory exposures of the same species to heavy metals. Although laboratory exposures are subject to criticism on the grounds that they do not correspond closely to natural conditions, they do make it possible to attribute changes to a particular pollutant, which is not often possible in the field.

Materials and methods

Field study

Windowpane flounder for the field study were collected by otter trawl using 30-minute tows at the three desig-

nated stations and held in running seawater aboard the boat until blood samples were taken, generally within 1 hour after the fish were collected. On occasion, because of inclement weather, it was necessary to return to the laboratory and sample the fish at dockside; in that case, the interval between capture and sampling was up to 4 hours.

The stations were sampled monthly unless inclement weather or boat repairs precluded sampling. Generally, blood samples were taken from 20 fish at each station; if fewer fish were obtained, sample numbers were necessarily smaller. Of 102 collections used, 67 consisted of 20 fish each, 33 of 10–19 fish, and one each of 8 and 9 fish. Respective lengths of fish sampled at Station 1, 2, and 3 were 26.7 ± 0.13, 25.0 ± 0.16, and 25.6 ± 0.15 cm. Hematocrit (Hct), hemoglobin (Hb), plasma osmolality, sodium, potassium, and calcium were measured on each blood sample. Prior to each fish collection, a bottom-water sample was collected for measurement of temperature, salinity, and dissolved oxygen. Four preliminary collections were made at each station in 1979; intensive sampling continued from May 1980 through April 1983.

Exposure studies

Windowpane flounder were exposed to mercury, copper, or cadmium in the laboratory. Fish used in the exposure studies were collected by otter trawl using 15- or 30-minute tows in the vicinity of Milford, Connecticut, and transported to the laboratory in running seawater. They were held at the laboratory for at least 2 weeks prior to exposure. In general, exposures were conducted during the colder months when the fish do not normally feed much. However, they were given small amounts of minced surf clam *Spisula solidissima* weekly. The fish measured 24.8 ± 0.21 cm in length and 158.4 ± 4.2 g in weight.

Three 60-day exposures were performed: the first used $HgCl_2$ at a nominal mercury concentration of 5 or 10 μg/L, the second used $CuCl_2 \cdot 2H_2O$ at a nominal copper concentration of 10 or 20 μg/L, and the third used $CdCl_2 \cdot 2½ H_2O$ at a nominal cadmium concentration of 5 or 10 μg/L. Measured concentrations were 5.1 ± 0.60 ppb and 12.7 ± 2.20 ppb for low and high cadmium concentrations, and 19.2 ± 1.4 for the high copper concentration. Background metal levels were below 1 μg/L for mercury, below 5 μg/L for copper, and below 1 μg/L for cadmium. The fish were exposed in 285-L fiberglass tanks filled to 225 L with sand-filtered Milford Harbor seawater by a proportional dilution apparatus (Mount and Brungs 1967). The diluter controlled the intermittent delivery of toxicant-containing or control seawater at a flowrate of 1.5 L every 2.5 minutes throughout the exposure period. This provided a flow of 864 L per day and an estimated 90% replacement time of 15 hours (Sprague 1969). The seawater was at ambient salinity during the exposures. The temperature was slightly above ambient because the water was held in the heated building during filtration and delivery.

Duration of the mercury exposure was 22 December 1979–20 February 1980. The salinity range during that time was 25.0–26.9‰. Temperature in the exposure tanks was 8°C at the beginning of the exposure, dropping to 3-4°C throughout most of the month of February when the exposure was completed. During the mercury exposure, each tank held 5 fish for a total of 20 fish per concentration and 20 controls.

The copper exposure ran from 7 January through 8 March 1983. Salinity during the exposure period was 24.4–26.4‰. Temperature was 9°C at the beginning of exposure, dropped to a low point of 6°C in mid-February, and gradually rose to 9°C at the end. Three tanks at each concentration held 4 fish per tank.

Duration of the cadmium exposure was 27 January–28 March 1984. Salinity range during that time was 22.6–25.9‰. Temperature was 6.5°C at the beginning of the exposure, rising to 8.5°C at the end. The lowest temperature recorded was 5.0°C on 3 February. Twenty fish were exposed per concentration, 5 fish per tank.

Blood chemistry

The parameters measured were hematocrit (Hct), hemoglobin (Hb), mean corpuscular hemoglobin concentration (MCHC), plasma osmolality, sodium, potassium, and calcium. Erythrocyte counts (RBC) and calculations of mean corpuscular hemoglobin (MCH) and mean corpuscular volume (MCV) were performed only on animals used in exposures.

Blood was collected from each animal by cardiac puncture using a 3-mL plastic syringe and a 20- or 22-gauge needle. The sample was transferred gently into an 8-mL glass vial containing 150 units of dried ammonium heparinate as an anticoagulant. Immediately following collection of the last blood sample, a portion of each blood sample was centrifuged at 12 000 g and the plasma frozen for later determination of osmolality, sodium, potassium, and calcium. The remaining whole-blood sample was used for the determination of hemoglobin, hematocrit, and erythrocyte counts. Hemoglobin was determined by the cyanmethemoglobin method using Hycel chemicals. Microhematocrits were determined following centrifugation for 5 minutes at 13 500 g. Erythrocyte counts were made in a hemacytometer; blood samples were diluted 1:200 with Yokoyoma's solution (Katz 1950). Plasma osmolality was determined with an

Table 1

Effects of 60-day exposure to mercury on blood of windowpane flounder *Scophthalmus aquosus* in Long Island Sound. Values are mean ± standard error, with number of samples in parentheses. Number of samples is often fewer than that of fish exposed because of clotting or pooling of samples.

		Mercury concentration	
Test	Control	5 μg/L	10 μg/L
Hematocrit (%)	22.00 ± 1.3 (17)	25.00 ± 1.4 (15)	24.00 ± 1.6 (18)
Hemoglobin (g/100 mL)	4.10 ± 0.2 (17)	4.30 ± 0.3 (15)	3.40 ± 0.2 (18)
Erythrocytes (10^6 cells/mm^3)	2.14 ± 0.17 (9)	2.13 ± 0.14 (9)	2.41 ± 0.29 (10)
MCV (μ^3/cell)	96.60 ± 5.7 (9)	109.80 ± 4.0 (9)	103.90 ± 9.1 (10)
MCH (pg/cell)	20.20 ± 1.6 (9)	21.10 ± 1.2 (9)	18.90 ± 1.2 (10)
MCHC (g/100 mL)	19.10 ± 1.0 (17)	18.40 ± 0.6 (15)	18.10 ± 0.5 (18)
Na (mEq L)	179.00 ± 3.9 (11)	181.00 ± 3.5 (14)	*199.00 ± 3.3 (13)
K (mEq/L)	8.21 ± 0.85 (11)	6.93 ± 0.66 (14)	8.52 ± 0.81 (13)
Ca (mEq/L)	4.95 ± 0.23 (11)	*3.91 ± 0.18 (14)	*3.60 ± 0.19 (13)
Osmolality (mOsm)	338.00 ± 7.7 (9)	328.00 ± 4.0 (14)	331.00 ± 2.9 (12)

MCV = Mean corpuscular volume
MCH = Mean corpuscular hemoglobin
MCHC = Mean corpuscular hemoglobin concentration
*Significantly different from controls ($P<0.05$).

Advanced 3L osmometer; the effect of the added heparin on osmolality was negligible. Plasma sodium, potassium, and calcium concentrations were measured with a Coleman 51 flame photometer. At times it was necessary to pool the small plasma samples, resulting in slightly fewer samples for plasma ions and osmolality. Mean corpuscular volume (MCV), mean corpuscular hemoglobin (MCH), and mean corpuscular hemoglobin concentration (MCHC) were determined using the following equations (Platt 1969):

MCV in μ^3/cell = 10 Hct/RBC
MCH in pg/cell = 10 Hb/RBC
MCHC in g/00 mL packed red cells = 100 Hb/Hct

Statistical differences were determined by one-way analysis of variance and the Scheffe test (Hicks 1973).

Results

Exposure studies

Results of the 60-day exposure of windowpane flounder to mercury are summarized in Table 1. Red blood cells in the species appear to be unaffected by mercury at the test concentrations used in this study. Control flounder had a mean hematocrit of 22 ± 1.3%, a mean hemoglobin of 4.1 ± 0.2 g/100 mL, and a red cell count of 2.4 ± 0.17 × 10^6 cells/mm^3. Following a 60-day exposure of the fish to 5 or 10 μg/L mercury, none of these variables differed signficantly from control values, nor did the indices calculated from the three variables (namely, MCH, MCV, and MCHC). The mean plasma sodium level in flounders exposed to 10 μg/L mercury was 199 ± 3.3 mEq/L, significantly higher than the control value of 179 ± 3.9 mEq/L. Plasma calcium decreased from the control value of 4.95 mEq/L to 3.91 ± 0.18 and 3.60 ± 0.19 m/Eq/L in animals exposed to 5 and 10 μg/L mercury, respectively. There were no significant differences between controls and mercury-exposed flounder in plasma potassium or osmolality (Table 1).

No significant difference was demonstrated between controls and animals exposed to either concentration of cadmium or copper in any of the parameters measured.

Field study

The data from each season were divided by sex and compared using the Scheffe test; no significant sex-related differences were noted. The data were grouped into four size-classes (<20.0 cm, 20.1–25 cm, 25.1–30.0 cm, >30 cm) and compared for each season; no significant size-related differences were noted during any season. Because of the lack of differences, data from both sexes and all size-classes are shown together.

Overall, windowpane flounder taken from Station 3 had significantly higher hematocrits and hemoglobin concentrations than did those taken from Station 1.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 2

Hematocrits of windowpane flounder *Scophthalmus aquosus* in Long Island Sound. Values are percent ± standard error, with number of fish in parentheses.

Station	Winter	Spring	Summer	Fall
1	[a,b]20.6 ± 0.9 (78)	[c]23.2 ± 0.3 (172)	[d]24.9 ± 0.4 (140)	23.8 ± 0.4 (139)
2	[b]22.1 ± 0.4 (105)	24.0 ± 0.3 (182)	24.6 ± 0.5 (132)	23.9 ± 0.5 (137)
3	[b]23.2 ± 0.6 (93)	[a,c]26.6 ± 0.4 (178)	[d]25.4 ± 0.4 (136)	[a]25.9 ± 0.4 (139)

[a]Significantly different ($P<0.05$) from all other stations in a given season.
[b]Significantly different from all other seasons at a given station.
[c,d]Significantly different pairs of seasons at a given station.

Table 3

Hemoglobin concentrations of windowpane flounder *Scophthalmus aquosus* in Long Island Sound. Units are g/100 mL ± standard error, with number of fish sampled in parentheses. No significant seasonal variations were demonstrated. Values from Station 1 are significantly lower than those from Stations 2 and 3; however, no contrasts between stations were significant when the data were separated by season.

Station	Winter	Spring	Summer	Fall
1	3.5 ± 0.13 (89)	3.6 ± 0.11 (173)	4.2 ± 0.11 (164)	3.6 ± 0.12 (133)
2	4.0 ± 0.13 (113)	4.0 ± 0.11 (188)	4.0 ± 0.12 (145)	3.8 ± 0.11 (149)
3	3.8 ± 0.14 (84)	3.9 ± 0.10 (169)	4.1 ± 0.10 (153)	4.2 ± 0.14 (150)

Table 4

Seasonal variations in blood chemistry of windowpane flounder *Scophthalmus aquosus* in Long Island Sound. Values are mean ± standard error. Because of the lack of significant differences between stations in these variables, data from all stations are combined.

Variable	Winter	Spring	Summer	Fall
MCHC (g/100 mL)	17.00 ± 0.04 (256)	15.60 ± 0.03 (508)	15.30 ± 0.04 (408)	14.40 ± 0.04 (419)
Sodium (mEq/L)	[a]186.00 ± 0.4 (285)	170.00 ± 0.3 (515)	[b]157.00 ± 0.3 (409)	[b]157.00 ± 0.3 (405)
Potassium (mEq/L)	[a]4.10 ± 0.18 (285)	[b]5.16 ± 0.14 (515)	[b,c]5.48 ± 0.15 (409)	[d]4.25 ± 0.16 (405)
Calcium (mEq/L)	4.22 ± 0.12 (285)	[a]4.43 ± 0.10 (515)	3.79 ± 0.10 (409)	[b]3.49 ± 0.11 (405)

MCHC = Mean corpuscular hemoglobin concentration.
[a,b]Significantly different pairs.
[c,d]Significantly different pairs.

When the data from each station were separated by season, the difference between Stations 1 and 3 in hematocrit was significant during the winter, spring, and fall (Table 2). When the data on hemoglobin levels were separated by season, the difference between stations for any particular season was not significant (Table 3). Variations in hemoglobin from season to season were not significant (Table 3). At each station, the hematocrits of flounders collected during the winter were significantly lower than those of fish collected at any other season (Table 2).

Seasonal means in MCHC ranged from 14.4 to 17.0. There were no significant differences either between stations or between seasons (Table 4).

Plasma sodium levels varied by season but not by station. Because of the lack of difference between stations, the data from the three stations were treated together. The mean sodium value for winter-collected animals at all stations was 186 ± 0.4 mEq/L; this is significantly higher than the summer and fall values, both of which were 157 ± 0.3 mEq/L (Table 4).

Plasma potassium levels varied significantly by season but not by station. The highest levels were found in the summer. The mean value for summer-collected animals of 5.48 ± 0.15 mEq/L was significantly higher than either the winter value of 4.10 ± 0.18 mEq/L or the fall value of 4.25 ± 0.16 mEq/L (Table 4).

Table 5

Plasma osmolalities of windowpane flounder *Scophthalmus aquosus* in Long Island Sound. Units are mOsm ± standard error, with number of fish in parentheses. Within each station, groups which are not significantly different are underlined.

Station	Winter	Spring	Summer	Fall
1	*392 ± 5 (89)	*387 ± 2 (167)	390 ± 2 (129)	*401 ± 2 (124)
2	377 ± 2 (109)	377 ± 2 (170)	393 ± 3 (113)	*389 ± 3 (118)
3	380 ± 2 (87)	374 ± 2 (176)	*383 ± 2 (134)	*377 ± 2 (132)

*Significantly different ($P<0.05$) from all other stations at a given season.

There were no significant differences between stations in plasma calcium levels. The only seasonal variation was a significant difference between the spring value of 4.43 ± 0.10 mEq/L and the fall value of 3.49 ± 0.11 mEq/L (Table 4).

Overall, plasma osmolalities of fish collected from Station 3 were significantly lower than those of fish collected from Station 1. When the data were separated by season, the difference between Stations 1 and 3 for each season was significant (Table 5). During the winter, spring, and fall, plasma osmolalities from Station 2 were also significantly lower than those from Station 1. In general, the lowest plasma osmolalities were found in the spring at each station; the highest, in summer or fall. None of the season-to-season variations in plasma osmolality at Station 3 were significant.

The mean salinity was 27.6‰ at Station 1, 27.9‰ at Station 2, and 26.7‰ at Station 3. The total range of salinity measured was 22.9–30.4‰. The difference between stations for a single month was rarely more than 2‰. Bottom temperatures are summarized in Figure 2. In general, station-to-station differences were slight. Dissolved oxygen concentrations are presented in Figure 3. Station 3 tended to have a low oxygen concentration during the summer. During the cooler months, differences between stations in dissolved oxygen were less pronounced. Station 1 is 5.5 m deep; Station 2, 15.2 m; and Station 3, 10.7 m.

Discussion

This investigation was undertaken in order to observe windowpane flounder blood chemistry in the field and to use a series of laboratory exposures in an attempt to explain the inter-station differences. However, the exposures actually provided only negative information on the causes of differences in blood chemistry observed in the field. The Interstate Sanitation Commission (unpubl.) reported a median copper concentration in the water column of western Long Island Sound of 12 μg/L; the highest reported copper levels were above 60 μg/L. This indicates that the exposure concentrations of 10 and 20 μg/L were realistic in terms of a polluted environment. Few water column cadmium concentrations were above 5 μg/L and the median was 1.0 μg/L. Therefore, the exposure concentrations of cadmium were realistic to slightly high. Mercury levels used in the exposures were high compared with those measured in Long Island Sound waters; the highest measured mercury concentration was 1.8 μg/L and the median was <0.1 μg/L, compared with exposure levels of 5.0 and 10.0 μg/L. The limited effects of mercury at a high exposure level and the lack of effects of cadmium and copper at more environmentally relevant water concentrations clearly demonstrated that the differences between stations cannot be explained by the effects of these metals. The lack of effects of the exposures in the present study does not diminish the possible usefulness of this type of approach. The exposures performed here were by no means comprehensive; a more extensive program of exposures might mimic the inter-station differences.

Bridges et al. (1976) reported changes in blood chemistry and, specifically, the development of anemia in winter flounder held in the laboratory for over 50 days. Anemia was not noted in such animals in the present study; hematocrits and hemoglobin levels of laboratory-held fish were typical of those of animals collected in the field during the same season. However, the plasma potassium levels of windowpane flounder used for the mercury exposure were somewhat higher than those of fish sampled immediately after collection; this may be the result of the length of time that the fish were held in the laboratory.

The geographical range of the field study was limited to stations at which monthly sampling was feasible. This limitation made it possible to describe seasonal

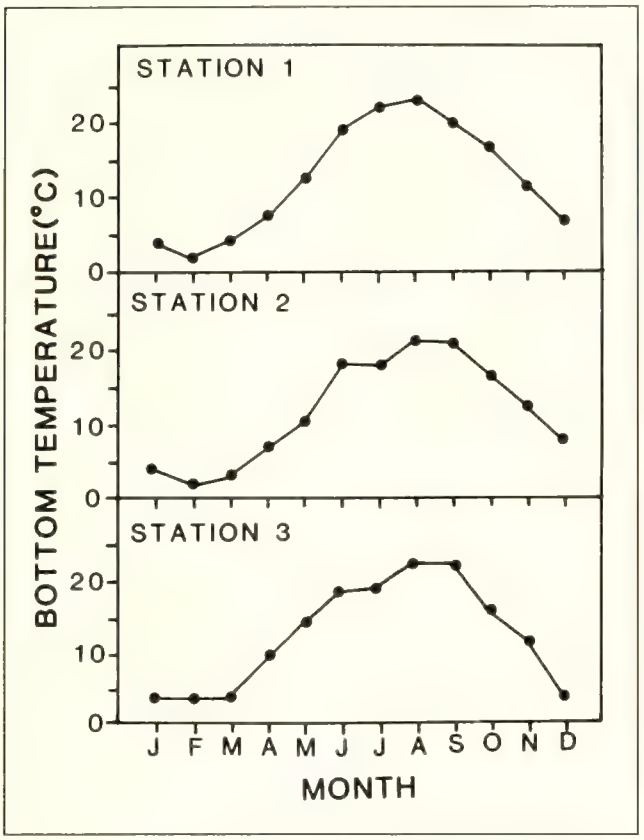

Figure 2
Yearly cycle of bottom temperatures at the three Long Island Sound stations. Each point is the mean of all samples taken from a given month and station throughout the study.

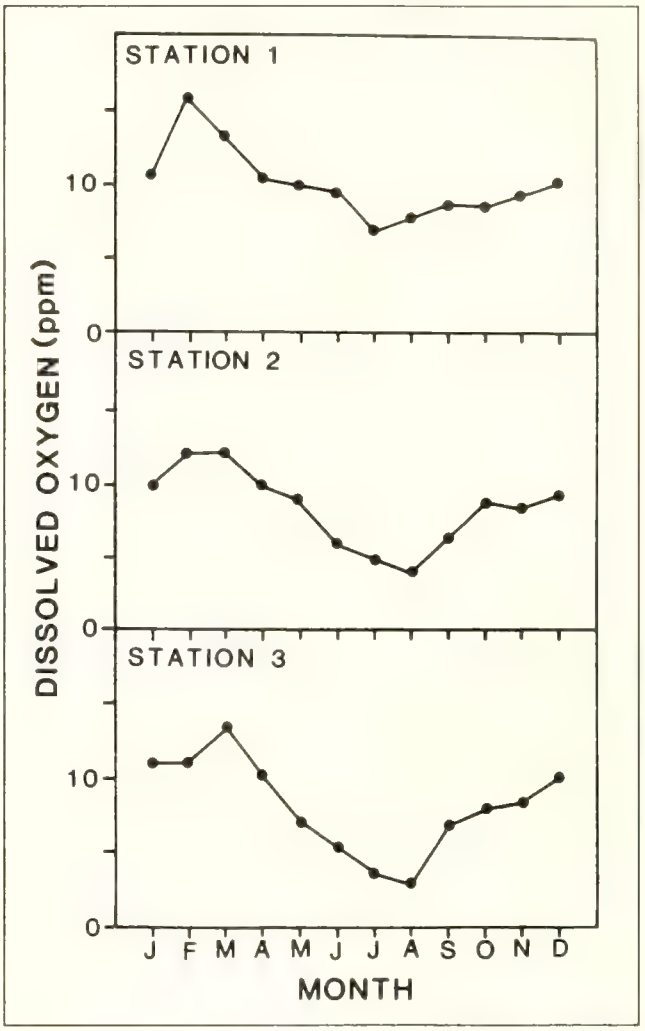

Figure 3
Yearly cycle of dissolved oxygen concentrations at the three stations in Long Island Sound. Each point is the mean of all samples taken from a given month and station throughout the study.

changes. Seasonal variations encompass a variety of parameters, including temperature, light, and nutrient availability. It was assumed that any variations which related to station rather than season were the result of differences in contaminant load. The low oxygen level at Station 3 during a portion of each summer may be indirectly a pollutant effect because low dissolved oxygen is often concomitant with organic pollution.

Mercury exposure produced more limited changes in windowpane flounder than in other species of fish exposed under similar conditions. Exposure to 10 μg/L mercury for 60 days produced no significant changes in the red cell component of windowpane flounder blood. Exposure of winter flounder *Pseudopleuronectes americanus* and striped bass *Morone saxatilis* to the same mercury concentration under similar conditions reduced hematocrit, hemoglobin, and red cell count by 18–48% of control values (Calabrese et al. 1975; Dawson 1979, 1982). The mercury-induced changes in plasma chemistry observed in this study paralleled those found in exposures of other species more closely than did the red cells. Both winter flounder and striped bass exhibited a significant increase in sodium and a decrease in calcium following mercury exposure, and winter flounder also had a drop in plasma calcium concentration (Dawson 1979, 1982). The lesser effects of mercury on the windowpane flounder suggest that this fish is generally less susceptible than striped bass or winter flounder or that the distribution of the metal within the animal differs from species to species. Pentreath (1976) reported that both gill and kidney accumulated high concentrations of mercury during the exposure of plaice *Pleuronectes platessa* L. to this metal. Accumulation in the gill and kidney would be likely to affect plasma chemistry; kidney accumulation may affect renal hematopoiesis as well.

This study produced no significant changes in windowpane flounder blood following copper exposure.

Other investigators have reported hematological effects of copper exposure in various fish species. Christensen et. al. (1972) reported significant increases in hematocrit and hemoglobin in the brown bullhead *Ictalurus nebulosus* following copper exposure. The exposure levels ranged from 27 to 107 μg/L, compared with our 10 and 20 μg/L, and the changes were noted in the fish exposed to 40–107 μg/L copper. It is possible that the lack of copper effects in the present study simply reflects a low exposure level.

The results of the cadmium exposure were similar to those obtained in an earlier exposure of the winter flounder *Pseudopleuronectes americanus*, to cadmium in this laboratory (Calabrese et al. 1975). In the earlier study, winter flounder were exposed for 60 days to 5 or 10 μg/L Cd, as were the windowpane flounder in the present study. No hematological changes were observed in winter flounder, although Na, K, and Ca were not measured. Larsson (1975) reported decreased hematocrits and hemoglobin concentrations following a 9-week exposure of the flounder *Pleuronectes flesus* L. to concentrations of cadmium as low as 5 μg/L. The same study demonstrated decreased calcium and potassium, but these were observed only at higher Cd concentrations.

Both the laboratory exposures and the field-sampling portion of this study suggest that the windowpane flounder is a hardy animal. The higher hematocrit and hemoglobin at the most polluted station compared with the least polluted station suggest an increase in hematopoiesis. The plasma osmolality, normally well below the osmolality of the surrounding water, was lower in fish collected from the most polluted station than in those collected from the cleanest station, indicating no loss of osmoregulatory ability. The limited effects of cadmium, copper and mercury exposures indicate that the species is not particularly vulnerable to these pollutants. These facts taken together suggest that the windowpane flounder at the most polluted station were subject to a stress, perhaps pollutant-induced, sufficient to challenge their metabolism, but a stress to which they were capable of adjusting.

Acknowledgments

The author thanks S. Schurman, D. Kapareiko, and D. Tucker for technical assistance.

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Abstract.—Trawl collections were made for Atlantic threadfin *Polydactylus octonemus* from 5 to 100 m in the Gulf of Mexico along a cross-shelf transect off Texas during October 1977–August 1981. Threadfin generally mature at 165–210 mm TL as they approach 7–9 months of age. Spawning primarily occurs in one period, mid-December–mid-March, and spans 45–120 days overall; 90% of successful spawning may occur in only 59% of that period. Threadfin in the northwestern Gulf range from <5 to 27 m depths in the demersal stage but are most abundant at <5 to 16 m. Young-of-the-year recruit in waters <5–16 m when 2–4 months old. Fish begin to disperse to deeper waters in early summer and form a positive size gradient from the estuaries seaward. Threadfin in the demersal phase are not abundant in the northwestern Gulf after 9–11 months of age and reach only 15 months there. Observed mean and predicted sizes were 135–165 mm TL at 6 months, 165–215 mm at 9 months, and 180–205 mm at 12 months. Fitted von Bertalanffy parameters were 2.17–2.92 (K, annual), 195–230 (L_∞), and −0.03–0.08 years (t_0). Maximum size in the demersal phase is 230 mm TL in the northwestern Gulf, but more typically only 200–205 mm. Typical maximum life span (t_L) is about 1 year but may exceed that if individuals survive in a pelagic stage after spawning. Apparent mean time and cohort-specific total annual mortality rates are 97–100% in the northwestern Gulf. Population dynamics parameters presented are termed apparent because of the unknown effects of recruitment, movements, random variation, gear selectivity, etc. Spawning grounds seemingly lie along the Outer Continental Shelf, slope, or further offshore, and currents of the cyclonic shelf gyre off Texas and western Louisiana transport the young to estuarine and inshore nurseries.

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Reproduction, Movements, and Apparent Population Dynamics of the Atlantic Threadfin *Polydactylus octonemus* in the Gulf of Mexico*

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The Atlantic threadfin *Polydactylus octonemus* occurs along continental shelves from Massachusetts to Brazil, and in the Gulf of Mexico (Breder 1948, Briggs 1958, Dahlberg 1975, Fischer 1978). Although uncommon on the Atlantic coast (Hildebrand and Schroeder 1928, Anderson and Gehringer 1965, Anderson 1968, Wilk and Silverman 1976), it is abundant in Gulf of Mexico (Gulf) coastal, surf, and estuarine waters (Hildebrand 1954, McFarland 1963, Chittenden and McEachran 1976). However, its annual abundance seems to fluctuate greatly (Reid 1956, Gallaway and Strawn 1974, Ogren and Brusher 1977).

Despite its abundance, the life history of *P. octonemus* has not been studied in detail, and little supporting data have been published. General notes occur in many faunal studies including Gunter (1938a, 1945), Reid (1955), Miller (1965), and Juneau (1975). These notes indicate *P. octonemus* is a small, inshore species that occurs from spring through fall in the northern Gulf and spawns from fall through spring.

Our paper describes maturation, spawning periodicity, bathymetric distribution, recruitment, movements, age determination and growth using length frequencies, maximum size, life span, mortality, and relationships of length-weight, length-girth, standard-total length and fork-total length of *P. octonemus* in the northwestern Gulf. It also discusses spawning areas and larval dispersal in relation to Gulf hydrography, as well as how recruitment, movements, and randomization affect parameter estimation and interpretation.

Materials and methods

Collections for *Polydactylus octonemus* were made from nearly 3000 trawl tows in 71 monthly or twice-monthly cruises, October 1977–August 1981, along a cross-shelf transect in the Gulf off Freeport, Texas (Fig. 1) aboard a chartered shrimp trawler. Gear used were twin 10.4-m (34-ft) trawls with a 4.4-cm stretched-mesh cod end and a tickler chain. Initial stations usually were located at depths of 9, 13, 16, 18, 22, 27, 36, and 47 m. Sampling was expanded to include stations at 5 and 24 m after November 1978 and at 55, 64, 73, 82,

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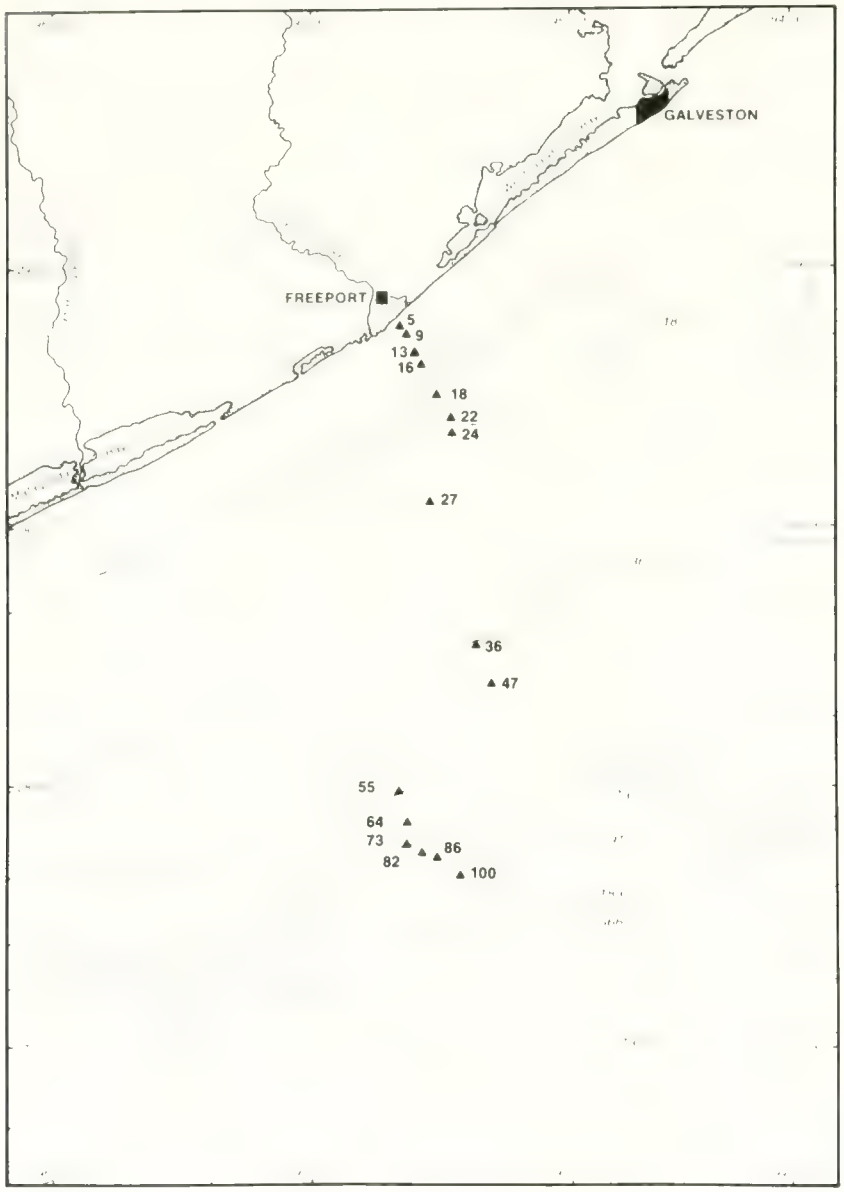


Figure 1
Location of sampling area off Freeport, Texas. Station depths and bathymetric contours are indicated in meters.

86, and 100 m after May 1979. Collections were made during the day through September 1978; thereafter, a day and a night cruise were usually made each month. Usually, two tows of 10 minutes bottom time were made at each depth, except that 8 were made at 16 m, 24 were made at 22 m, and only 1 tow was made at most depths prior to October 1978. We emphasize our spatial sampling design was a single, cross-shelf transect from a sampling frame that encompassed much of the northern Gulf.

All *P. octonemus* were culled from the catch, measured to the nearest millimeter total length, fixed in 10% formalin, and then preserved in 70% ethanol. All individuals collected January–December 1979 were processed to determine the following: total length (TL), fork length (FL), standard length (SL), girth at origin of the dorsal fin (G), total weight (TW), gonad weight (GW), and sex and gonad maturity stage. If available, 200 fish were randomly selected for similar processing in all other months, except standard length and girth were not recorded. Gonad maturity (Table 1) was determined by a modification of the Kesteven classification (Lagler 1978). Fish in the Early Developing and later stages were considered mature to calculate maturity curves (Bowering 1983), which indicate the length when half were mature (M_{50}). Gonadosomatic indices (GSI) were calculated for individual fish as: GSI = 100 GW/TW.

Age in years was determined by length-frequency analysis, e.g., the modal group progression analysis modification (Jearld 1983) of the Petersen Method (Lagler 1956). Knowing from this that essentially all

Table 1

Descriptions of gonad maturity stages assigned to *Polydactylus octonemus*.

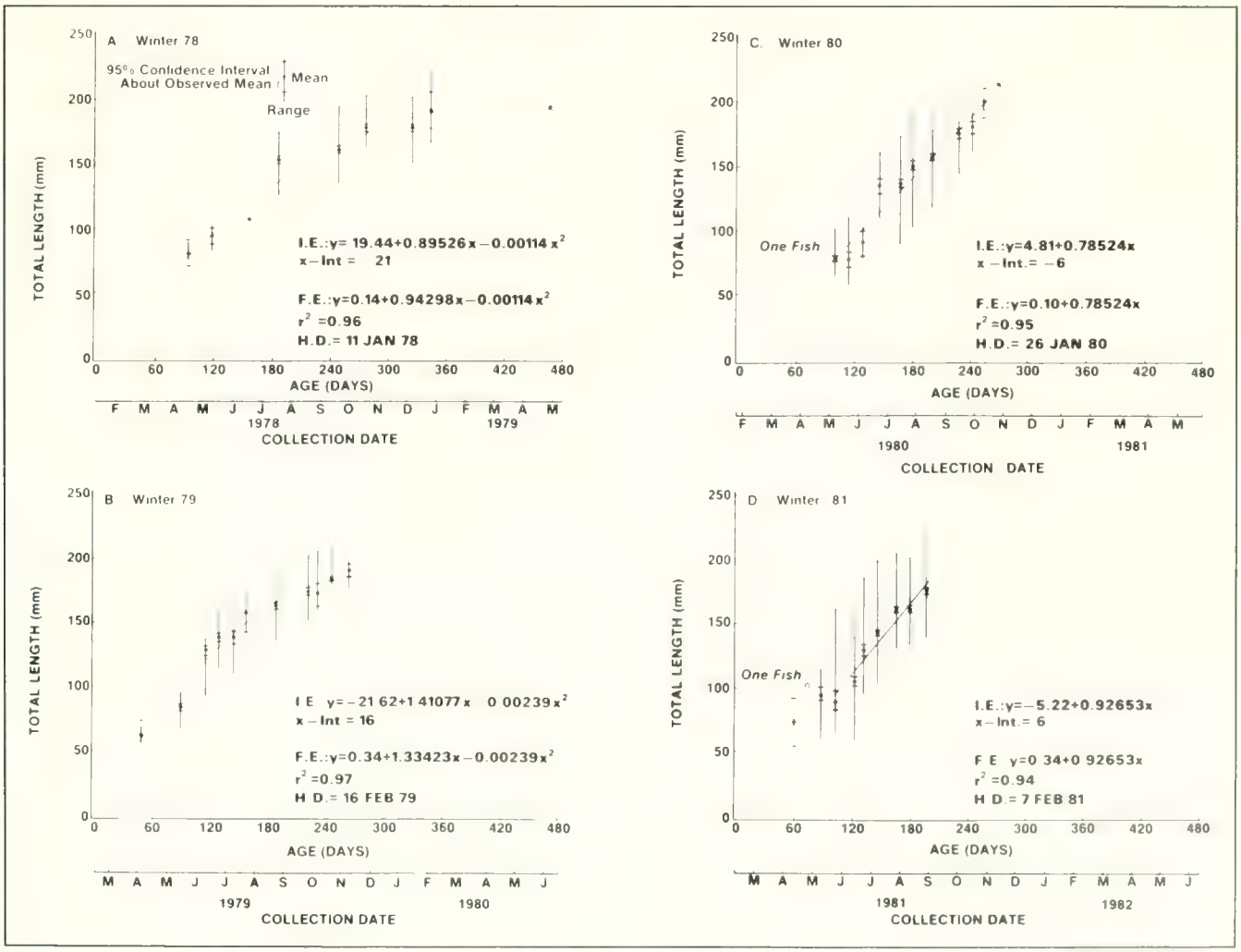
Stage and name	Description
1 Immature	Sex undetermined; gonads small or not visible.
2 Maturing Virgin	Sex distinguishable; gonads thin, occupy <10% of body cavity; eggs not visible.
3 Early Developing	Sex distinguishable to naked eye; gonads not flat, occupy 10–25% of body cavity; eggs opaque if present, not visible to naked eye.
4 Late Developing	Gonads occupy 25–50% of body cavity; opaque eggs present, visible to naked eye.
5 Gravid	Gonads occupy >50% of body cavity; up to 50% of eggs translucent.
6 Ripe	Gonads occupy >50% of body cavity; >50% of eggs translucent.
7 Spawning/Spent	Ovaries flaccid, completely or partially empty.

fish were age 0, we forced through the origin a regression to approximate age in days at observed sizes; this procedure is detailed under the methods used to calculate hatching dates. Cohorts (year classes) were specified on length-frequency figures by the season and year when they were hatched, e.g., winter 1981. Arithmetic means were used to describe central tendencies of length for each cruise, because length frequencies within each cohort were generally normally distributed.

Descriptions of spawning periodicity (beginnings and ends) using length frequencies assumed the following size and age combinations predicted from regressions of total length on age (Fig. 2): 25–40 mm TL at 1

Figure 2

Mean observed and predicted sizes at age (days) for *Polydactylus octonemus* cohorts with a summary of the iterative process used to calculate final hatching dates (H.D.) and set time-scales for final growth equations (F.E.). Initial growth equations (I.E.) were scaled to a 1 February hatching date. All regressions are significant at $\alpha = 0.005$. The first two and three collections of the 1980 and 1981 cohorts, respectively, were deleted from calculations; see text on "Maturation and Spawning Periodicity" for explanation.



month, 45–70 mm at 2 months, 70–100 mm at 3 months, and 95–125 mm at 4 months, depending upon cohort. These sizes were reasonable because growth averaged 28–32 mm/30 days at 3–6 months of age in May–July (Dentzau 1985).

Apparent duration of the overall spawning period was approximated following Geoghegan and Chittenden (1982), as

$$\frac{\text{Time-specific mean size range early in life}}{\text{Mean growth/day early in life}}$$

Calculations were based on fish collected early in life, i.e., May–June; too few were collected before then (1–4 fish/cruise in March and April) to estimate growth. For the numerator, time-specific size range was estimated for each cohort as the mean of the 99% confidence intervals for observations in that period. For the denominator, individual growth increments were estimated as the difference between (1) observed mean total lengths on successive dates and (2) total lengths on successive dates predicted from regressions. Individual estimates of growth/day were then made as the individual growth increment divided by the time between collection dates. Mean growth/day early in life was then estimated as the average of individual growth/day values between successive collections during May–June. Dentzau (1985, table 3) details these calculations. Calculations were also made using 90% confidence intervals to compare how much successful spawning occurred in a period shorter than the overall period.

Hatching dates used to approximate time scales to calculate growth were determined by a one-step iteration process following Standard and Chittenden (1984). An initial hatching date of 1 February was used to start the approximation, because fish 50–90 mm, assumed to be 2–3 months old, first appeared in March–April. Quadratic regressions of total length on age in days after 1 February were then used as models to estimate an initial $\bar{x}$-intercept for each cohort; linear regression was used if the quadratic term was not significant at $\alpha = 0.05$. Final hatching dates were calculated by using the $\bar{x}$-intercept for each cohort to readjust the initial x-variable (time) scale, so each final growth curve passed through the origin (Fig. 2).

Recruitment patterns and movements in the Gulf were determined by analyzing length frequencies and catch-per-unit-effort against depth at specified "seasons" (months) of the year; length-frequency data from Galveston Bay, Texas (Gallaway and Strawn 1974), extended our analyses to estuaries. We use the words "recruit" and "recruitment" in two ways: (1) to describe movement to areas by young *P. octonemus* descending to the bottom from their pelagic early stages, and (2) horizontal movements from estuaries

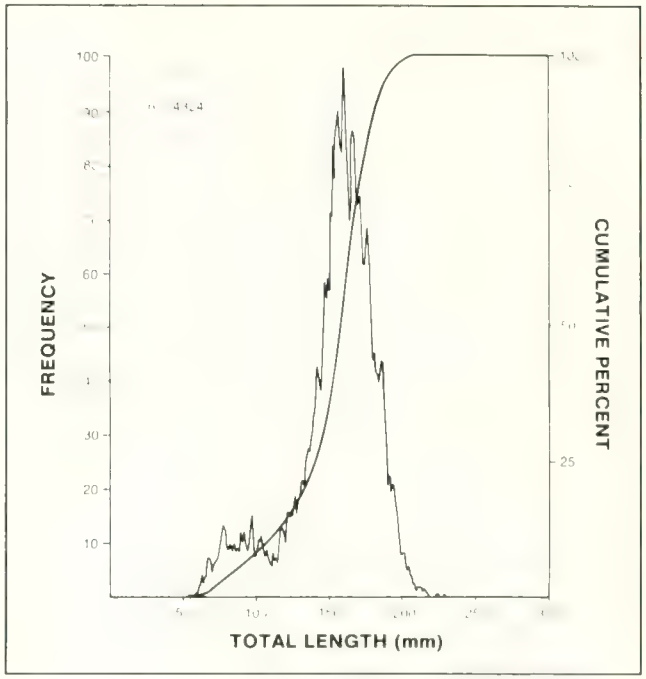


Figure 3
Length frequencies and cumulative percentage of all *Polydactylus octonemus* collected off Freeport, Texas, October 1977–August 1981.

to the Gulf, or within the Gulf, by fishes already in the exploited phase. The former conforms to Beverton and Holt's (1957) meaning of recruitment (t_r), because these areas are generally exploited, and to Beverton and Holt's (1957) and Ricker's (1975) meaning (t_c), because fish also then enter the exploited phase of life. Some gear selection for older, larger fish may occur as part of these processes.

Typical maximum life span was approximated by the Beverton-Holt model parameter t_L (Gulland 1969), and typical maximum size was approximated as a corresponding length (l_L) following the definition that only 0.5–1.0% of the catch exceeds age t_L (Alverson and Carney 1975, DeVries and Chittenden 1982). Values of l_L were calculated from the cumulative frequency for all fish captured (Fig. 3). Specific values of t_L were calculated from l_L by solving for time in von Bertalanffy (Gulland 1969) and regression growth equations (Fig. 2).

Time and cohort-specific total annual mortality rates ($1 - S$) were calculated using $S = N_t/N_0$, where S = rate of survival, and N_t and N_0 are the numbers of fish at age each month or per tow. Observed estimates were compared against theoretical values calculated from the expression $\bar{Z} = 4.6/\text{number of years in life span}$ (Royce 1972:238). Total mortality rates, typical maximum life spans, maximum sizes, sizes at age, spawning period durations, and von Bertalanffy parameters

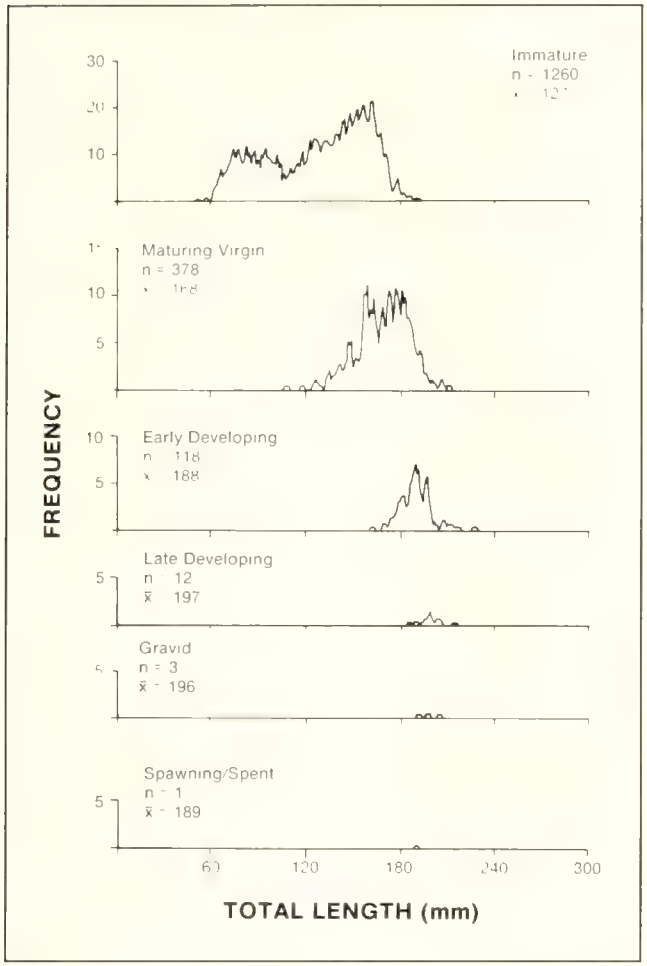


Figure 4
Length frequencies of immature and female *Polydactylus octonemus* by gonad stage.

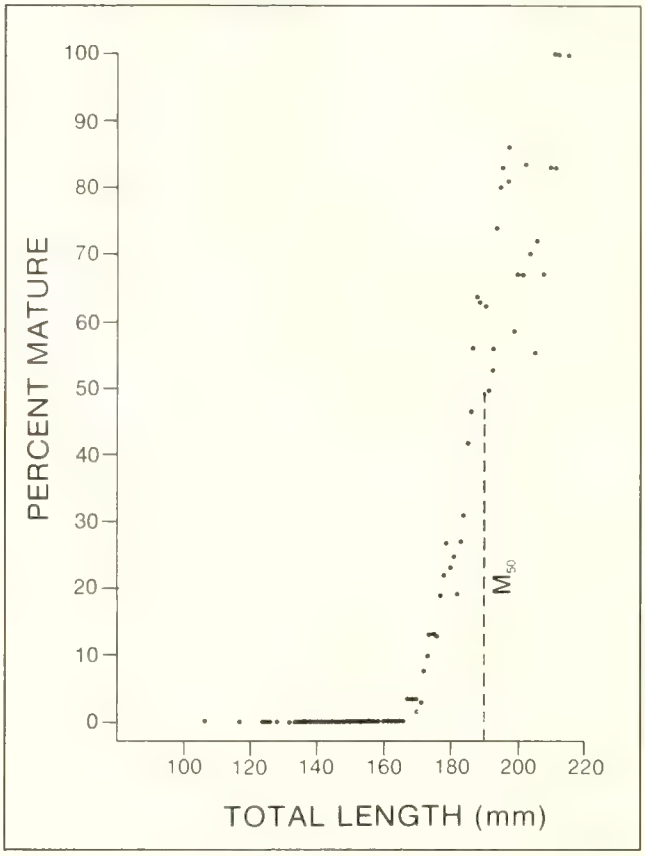


Figure 5
Percentage of mature female *Polydactylus octonemus* as a function of size.

presented were termed apparent, because they may have been affected by recruitment of larger young from estuaries to the Gulf, by emigration and/or gear avoidance of fish about age I, or by a change from demersal to pelagic behavior; if so, they overestimated mortality, K, and spawning period durations and underestimated life spans, maximum sizes, average sizes at age, and L_∞.

Von Bertalanffy parameters were calculated using Fabens' (1965) program and the same data used in TL on age regressions (Fig. 2). These points described a curvilinear regression and evidenced an asymptote, so they met the minimum requirements for a von Bertalanffy fit (Knight 1968, Gallucci and Quinn 1979). Unless stated, all length frequencies were moving averages of three and all lengths were total length. The symbol "?L" was used for instances where the type of length was not reported. Conversions between standard, fork, and total lengths used regressions presented herein.

Results

Maturation and spawning periodicity

Polydactylus octonemus begin to mature at 165–210 mm in late summer–early fall. Sex usually could be determined by eye at 165 mm as many females entered the Early Developing stage (Fig. 4). Fish entered later stages at 180–210 mm. M_{50} was 185–195 mm, about 7–9 months old (Fig. 5), in agreement with gonad-stage length frequencies.

Little somatic growth seemingly occurs after *P. octonemus* enter later stages of gonad development. Mean sizes were 188 mm in the Early Developing stage (Fig. 4), 197 mm when Late Developing, and 196 mm when Gravid. The only fish collected in the Spawning/Spent stage was 189 mm. Minimum and maximum sizes remained constant after the Early Developing stage.

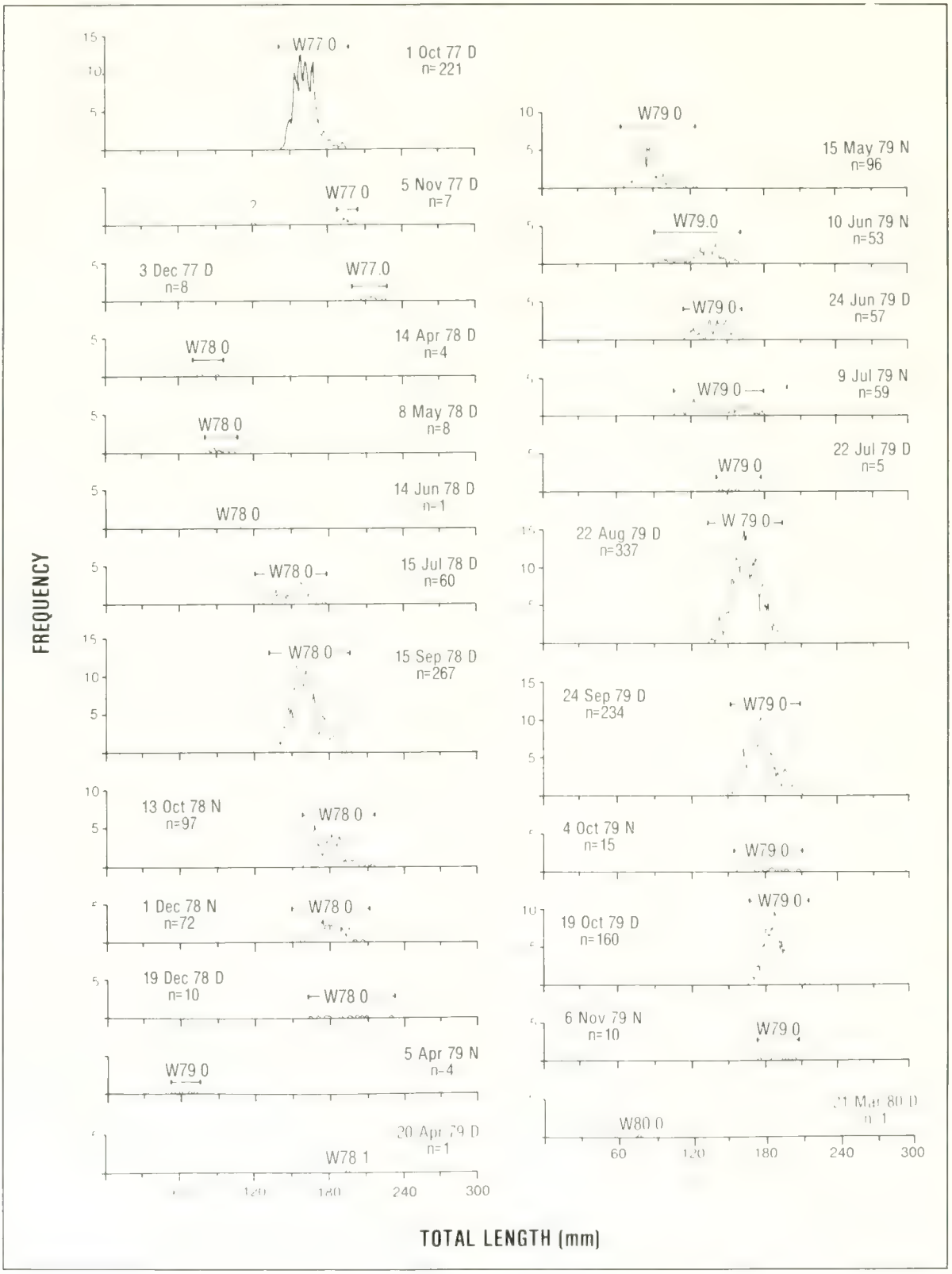


Figure 6

Monthly length frequencies of *Polydactylus octonemus* off Freeport, Texas, in day (D) and night (N) cruises. Bars in each panel depict cohort size ranges. The letter and first two digits above or within a bar indicate cohorts; the digit to the right of the decimal, age in years.

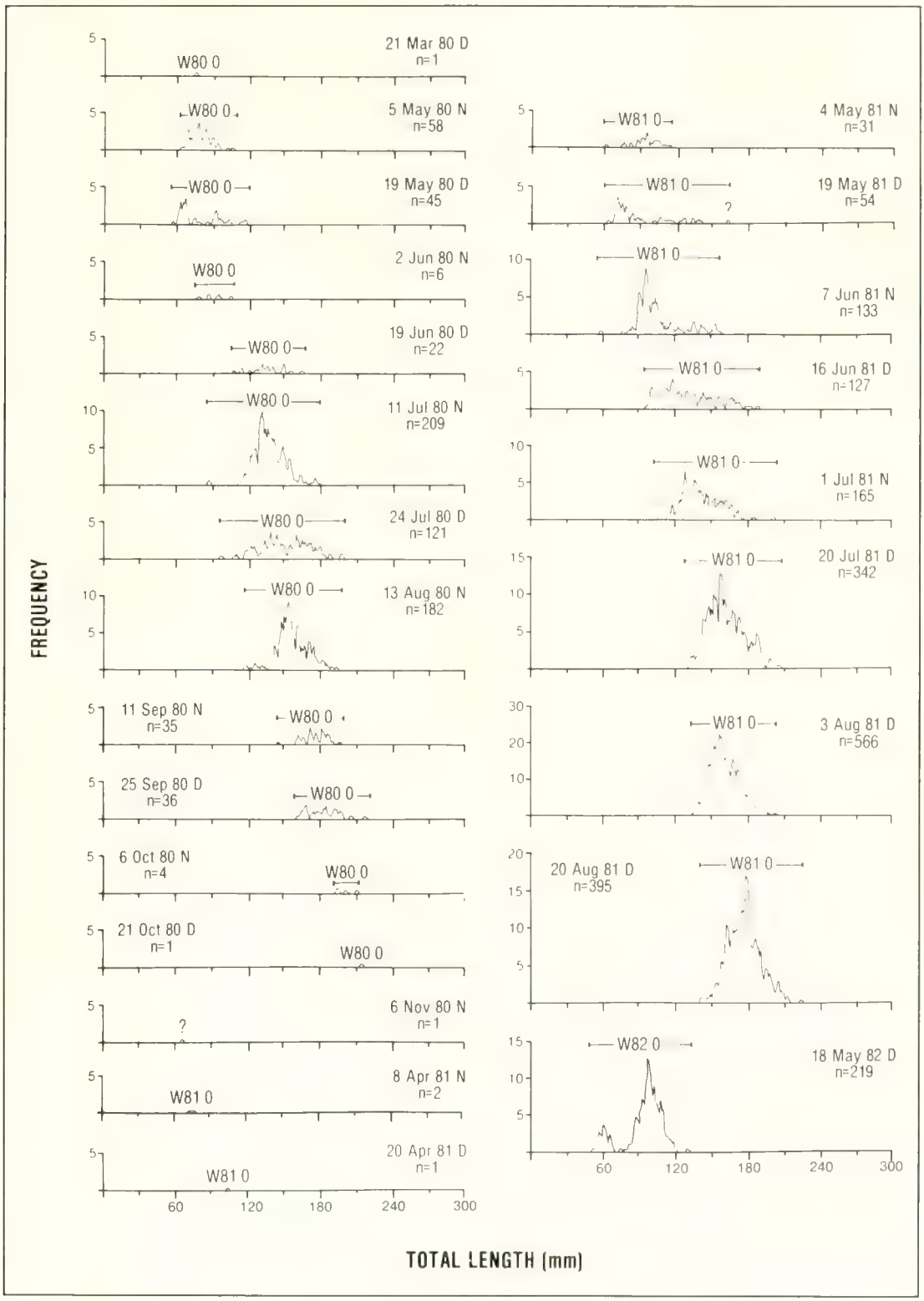


Figure 6 (continued)

Polydactylus octonemus primarily spawn in one discrete period from mid-December through mid-March. The well-defined modes in length frequencies from throughout the study (Fig. 6) suggest spawning occurred in one discrete period. Major spawning must have occurred during mid-December–mid-March, because small, young fish recruited mainly during mid-March–mid-May each year, e.g., fish 75–105 mm and

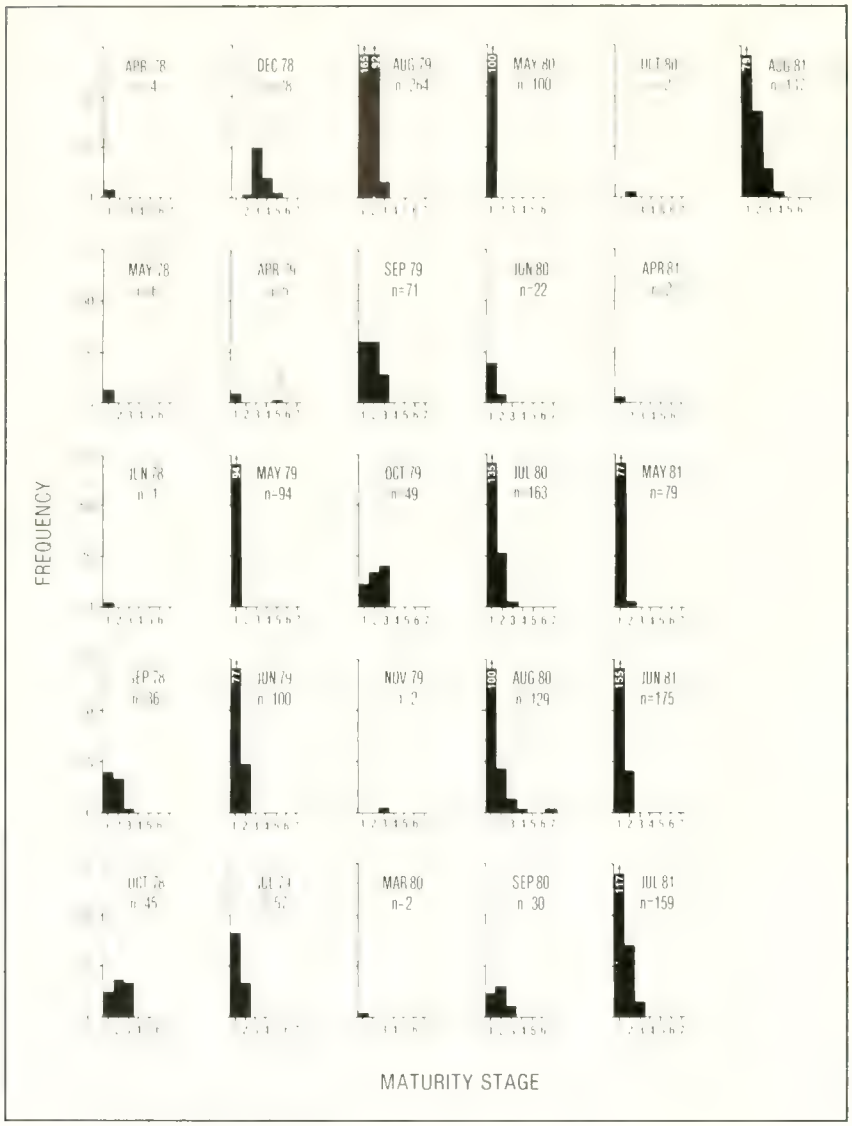


Figure 7
Monthly gonad maturity stages (defined in Table 1) of immature and female *Polydactylus octonemus*.

3–4 months of age recruited in abundance in mid-April–early May 1978, fish 50–70 mm and 2 months old in early April 1979, fish 65–115 mm and 2–4 months old in mid-May 1979, fish 75 mm and 3 months old in mid-March 1980, fish 55–115 mm and 2–4 months old in May 1980, and fish 60–115 mm and 2–4 months old in early April–early May 1981. Few fish 50–115 mm were collected from late August through February, indicating little spawning during late April–late October or November.

Calculated hatching dates were 11 January 1978, 16 February 1979, 26 January 1980, and 7 February 1981 for the 1978–1981 cohorts, respectively (Fig. 2). Other dates could have been calculated depending on data points included; however, the basic spawning period and coefficients of determination would be similar (Dentzau 1985). We deleted the earliest two collections in 1980 and earliest three in 1981 from calculations because mean sizes in these collections were as large or larger than those in subsequent ones and may have reflected incomplete recruitment or gear selection for larger fish, causing an upward size bias.

Gonad maturity data support the major mid-December–mid-March spawning period indicated by length frequencies. Except for one gravid age-I fish collected in April 1979, all fish collected in March–June were immature or maturing virgin (Fig. 7); none were in the Early Developing or later stages. Early and/or Late Developing stage fish were most common in October–December. Except for the one individual caught in April 1979, gravid fish were collected only in December as they approached age I. No ripe fish were collected, and few were gravid or late developing. Mean and/or maximum GSI values, although usually low, were high-

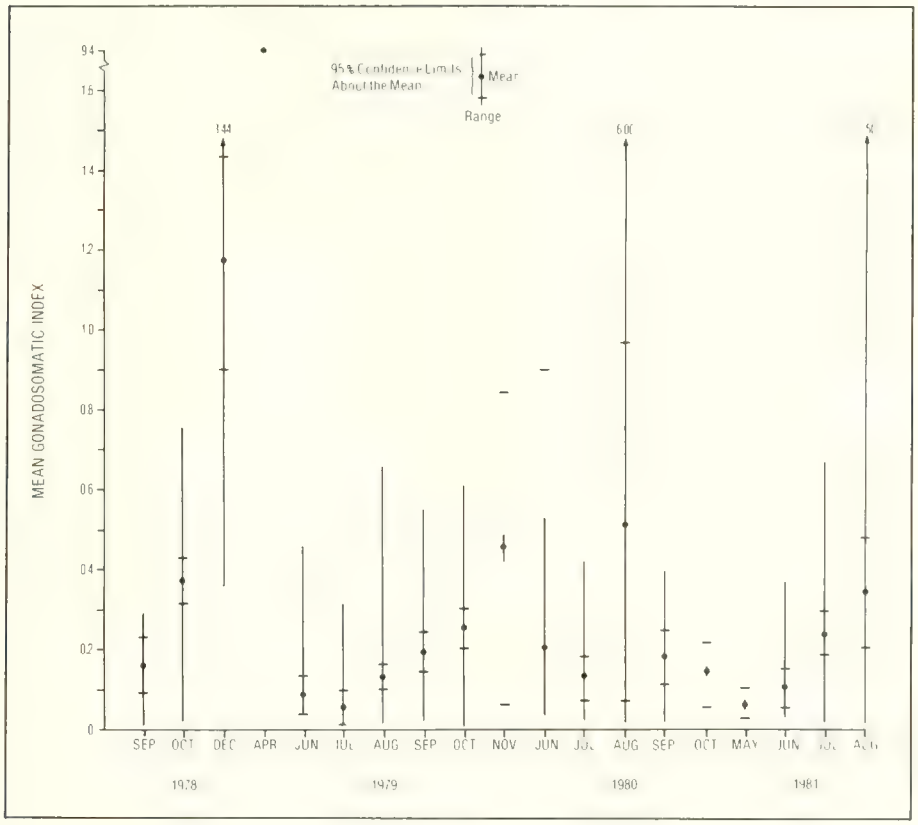


Figure 8
Monthly mean gonadosomatic indices, ranges, and 95% confidence limits about means for female *Polydactylus octonemus*, September 1978–August 1981.

est November–December (Fig. 8), except in August 1980 and 1981, when the few late-developing fish greatly skewed the means, and in mid-April 1979, when one age-I fish was gravid. The latter fish suggests some spawning in April and possibly May.

The apparent overall spawning period spans 45–120 days. Calculated overall spawning periods were 144 and 80 days in 1978, 53 and 80 days in 1979, 46 and 103 days in 1980, and 64 and 121 days in 1981 based on respective observed and predicted growth/day values. The broad 144-day interval for 1978 was based on only 9 fish and may be unreliable. Ignoring that value, spawning encompassed a 45–120 day interval which brackets the 90 day duration length frequencies indicated.

A large fraction of the successful spawning may occur in a period much shorter than the calculated overall spawning period duration. Using mean 90% instead of 99% confidence limits for observations, spawning periods were 78 and 43 days in 1978, 33 and 50 days in 1979, 27 and 60 days in 1980, and 40 and 76 days in 1981, based on respective observed and predicted growth/day values. On average, the duration estimated using 90% confidence limits was 59% of that using 99% limits. This suggests most spawning occurs in a relatively small part of the overall spawning period.

Cohorts are apparently produced by fish that first spawn when 10–14 months old, assuming the hatching dates and sizes at early age noted previously. Spawning at 10–14 months of age is supported by (1) the disappearance from collections of all but one fish sometime during late October–late December when 9–11 months old (Fig. 6), (2) the occurrence of large mean and maximum GSI values in October–December (Fig. 8), and (3) the collection of early developing and more sexually mature fish during September–December (Fig. 7).

Polydactylus octonemus exhibit a sex ratio of 1.00 male to 1.78 females. This ratio was observed in 800 fish and differed significantly from 1:1 ($\chi^2 = 64.98$, $\alpha = 0.05$, df = 1).

Bathymetric distribution, recruitment, and movements

Polydactylus octonemus in the northwestern Gulf occur from <5 m depths to at least 27 m off Freeport. Only one specimen was collected deeper than 27 m, a 75-mm fish at 86 m in April, which may represent a pelagic young captured as the net was being retrieved. Greatest abundance generally occurred at 5 m, the shallowest depth occupied (Fig. 9), except in 1978 when this depth was occupied only in December, a time when

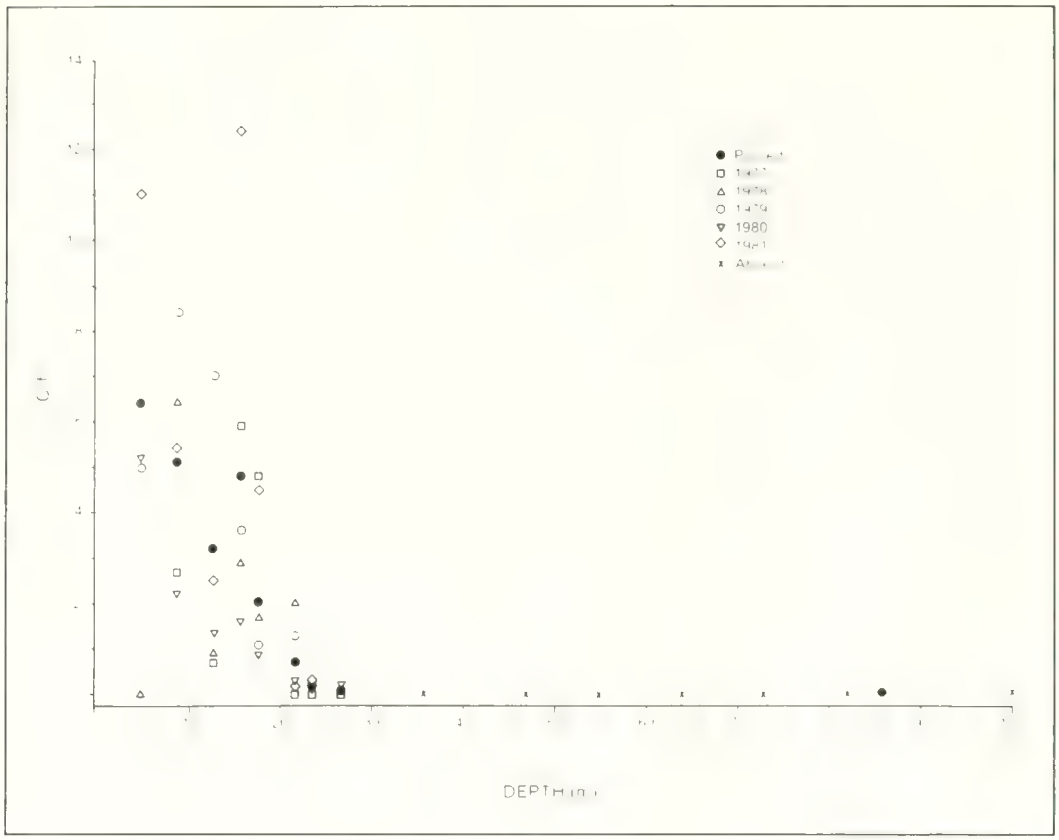


Figure 9
Catch/effort (mean number/10-min tow) by depth for *Polydactylus octonemus* off Freeport, Texas, each year and pooled, October 1977–August 1981. Tows in January and February were excluded in calculating effort because no fish were captured then.

fish had already begun to move offshore as noted below. Abundance was generally high at 9–16 m, although it often declined with increasing depth in this range. Abundance declined sharply between 18 and 22 m.

Young-of-the-year *P. octonemus* in the northwestern Gulf recruit to estuaries and coastal waters <5–16 m deep. Many young recruited to Galveston Bay in April and May when 50–110 mm (Fig. 10). In the Gulf, recruitment was greatest at the shallowest depths occupied. Fish 50–120 mm and 2–4 months old mainly recruited to 5–9 m in March–May, although some recruited as deep as 16 m (Fig. 11A, Table 2). Fish were most abundant at 5 m. Their abundance declined with increasing depth and was very low deeper than 13–16 m. Only one recruit was taken deeper than 16 m, the 75-mm fish at 86 m in April that may have been in a pelagic stage.

Polydactylus octonemus gradually disperse to deeper water in early summer and thereafter. Few age-0 fish were captured deeper than 9–13 m in April and May, but they were found at 18–27 m in June and were abundant at 16 m in July (Table 2). This gradual offshore dispersal is supported by the size gradient that existed seaward from Galveston Bay in June–December (Table 3), i.e., the smallest mean sizes were usually in Galveston Bay and the shallowest Gulf depths.

Larger *P. octonemus* lead the offshore dispersal. Minimum sizes were similar at each depth in the Gulf and in Galveston Bay during May (Fig. 10, 11A). In contrast, size compositions showed gradients of increasing size with depth in June, July, August, September, and October, suggesting larger, presumably older, fish move offshore first (Fig. 11A,B,C; Table 3).

Peak abundance of *P. octonemus* shifts towards deeper waters as they disperse offshore. Abundance was greatest by far at 5–9 m in May and June, then included 13 and 16 m in July as fish dispersed offshore (Table 2). Abundance peaked at 16 m in August and September, although fish were abundant from 5 or 9 to 18 m, and at 16–24 m in October (Table 2).

Polydactylus octonemus abandon estuaries and inshore portions of the Gulf (<5–9 m) in late fall and occupy only the offshore portions (13–24 m) before disappearing in November and December. Two fish at 9 m in November were the only individuals captured shallower than 13 m in the Gulf in November and December (Table 2), although peak abundance was at 5–9 m in May and June. Gallaway and Strawn's (1974) data show a similar abandonment of estuaries by late fall (Fig. 10).

Polydactylus octonemus were most abundant in July–September and least abundant November–April

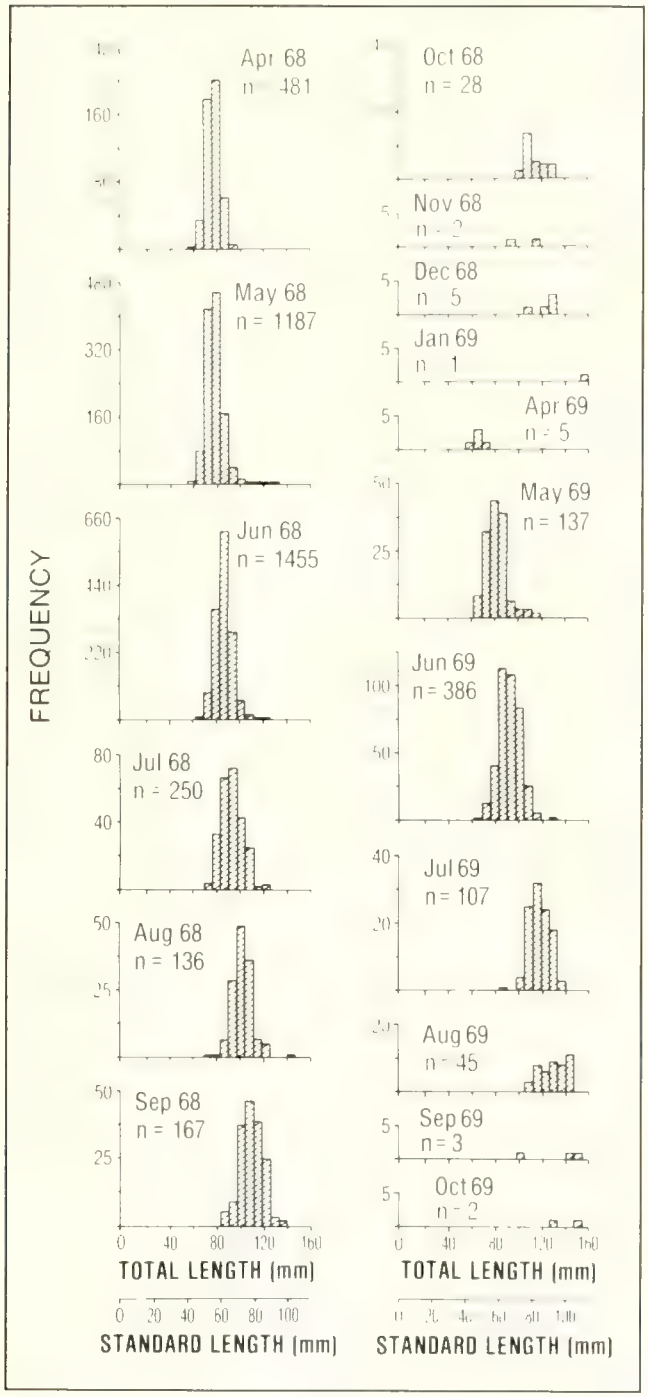


Figure 10

Monthly length frequencies of *Polydactylus octonemus* in Galveston Bay, Texas, 1968 and 1969. Adapted from seine and trawl data of Gallaway and Strawn (1974); length frequencies are not moving averages of three.

(Fig. 12). Usually no *P. octonemus* were captured December–February.

Age determination and growth

Only one cohort of *P. octonemus* usually occurs at any one time in the northwestern Gulf. The only exceptions to this we found were in April 1979 when two cohorts appeared, albeit on separate cruises, and possibly in November of 1977 and 1980 (Fig. 6), when the second cohort was represented by only one individual.

Polydactylus octonemus is not abundant in the demersal phase in the northwestern Gulf after 8–11 months of age and apparently reaches only 15 months. Cohorts were present only until their first November or December after which they were not captured again (Fig. 6), except for the 194-mm fish in April 1979 that was the only fish older than 12 months.

Apparent growth of *P. octonemus* varied between cohorts, but observed mean sizes, and von Bertalanffy and quadratic regression predictions, averaged 135–165 mm at 6 months, 165–215 mm at 9 months, and 180–205 mm extrapolated to 12 months (Table 4). Regardless of the growth model, for a given cohort, predicted sizes agreed within 6 mm or less at 6 and 9 months and within 11 mm at 12 months.

Fitted von Bertalanffy equations were:

$$(1978): l_t = 195.2[1 - e^{-0.007999(t-30.40)}];$$

$$\text{annual } K = 2.92; \text{ annual } t_0 = 0.0833$$

$$(1979): l_t = 230.4[1 - e^{-0.005955(t-11.69)}];$$

$$\text{annual } K = 2.17; \text{ annual } t_0 = -0.0320$$

where l_t = TL in millimeters at time t in days.

Maximum size, life span, and mortality

Polydactylus octonemus in the demersal phase apparently reach a maximum size of about 230 mm in the northwestern Gulf but more typically only 200–205 mm. The largest of 4324 specimens collected was 229 mm; 99% were <202 mm and 99.5% were <206 mm (Fig. 3). The latter two sizes estimate an apparent l_L.

The apparent typical maximum life span in the demersal phase of *P. octonemus* in the northwestern Gulf is only 1 year. A value of $t_L = 1$ seems reasonable because (1) l_L values of 202 and 206 mm can be substituted into hatching-date regressions and von Bertalanffy equations to predict values of 0.69–1.00 year; (2) observed and predicted mean sizes at 9 months are 165–215 mm and predicted sizes at 12 months are 180–205 mm; (3) the largest specimen was about 11 months old when collected in December 1978; and

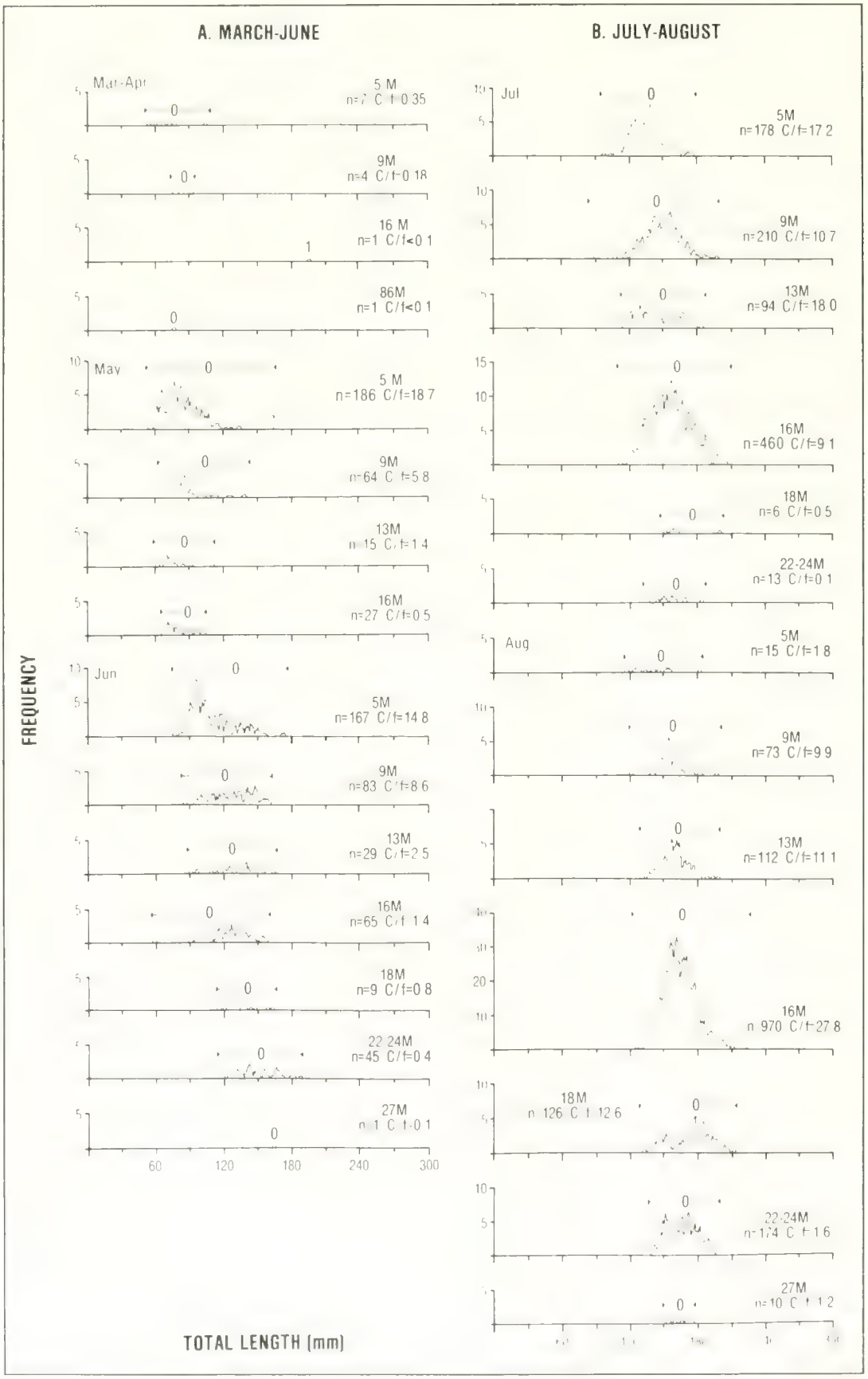


Figure 11
Length frequencies by depth for *Polydactylus octonemus* off Freeport, Texas, in March–June (A), July–August (B), September–October (C), and November–December (D). Data in each panel were pooled over the period October 1977–August 1981.

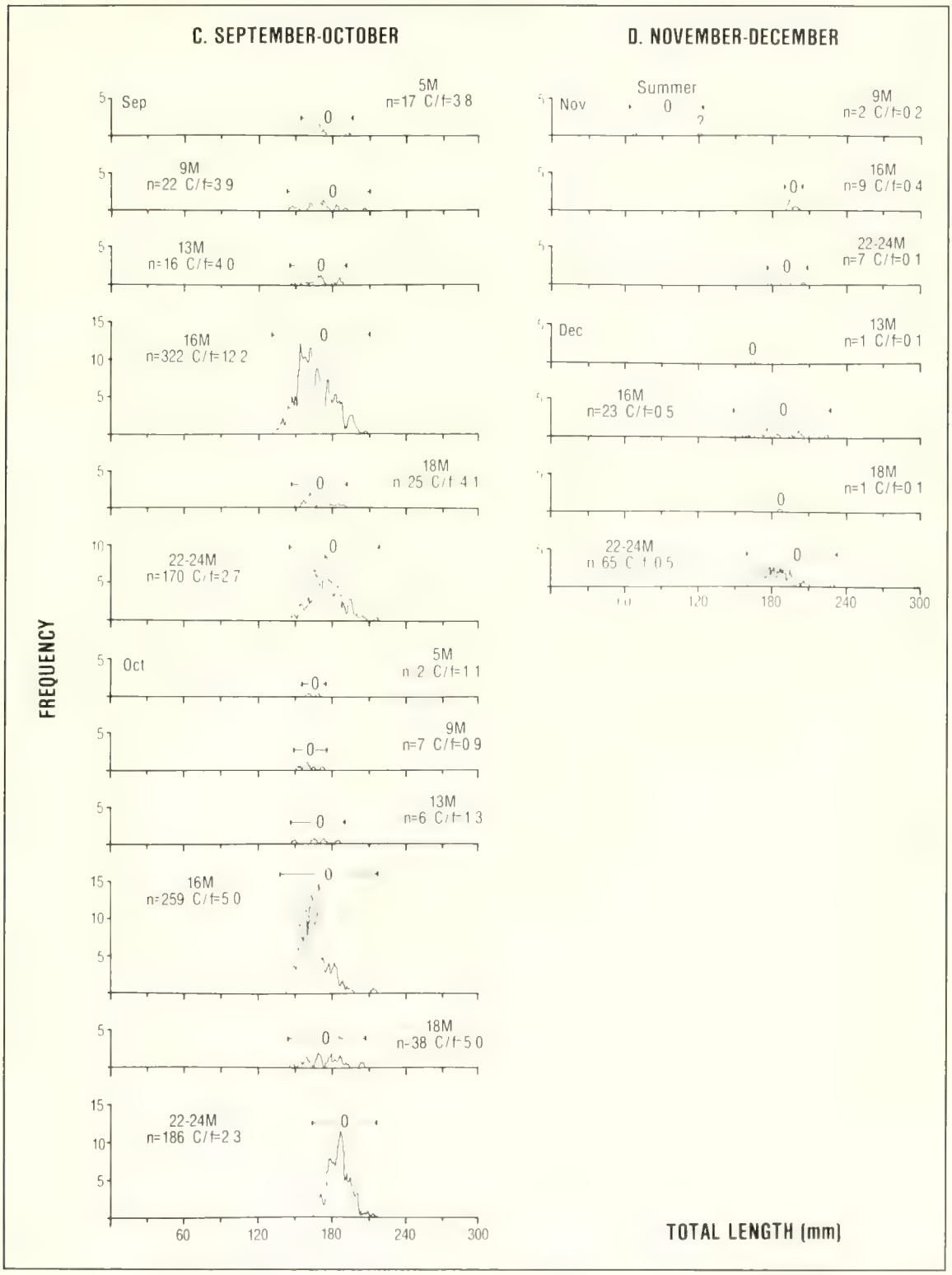


Figure 11 (continued)

(4) *P. octonemus* almost completely disappeared from trawl catches off Freeport at 9–11 months of age. The collection of one specimen seemingly 15 months old in April 1979 (Fig. 6) suggests a few age-I fish survive and remain in the white shrimp community, an inshore fauna described by Hildebrand (1954) and Chittenden and McEachran (1976). However, this would not greatly affect our estimate of t_L.

Table 2

Monthly catch/effort (mean number/10-min tow) of *Polydactylus octonemus* by depth off Freeport, Texas.

	Depth (m)						
Period	5	9	13	16	18	22–24	27
Mar.–Apr.	0.4	0.2	0.1	0.1	0	0	0
May	18.7	5.8	1.4	0.5	0	0	0
June	14.8	8.6	2.5	1.4	0.8	0.4	0.1
July	17.2	10.7	18.0	9.1	0.5	0.1	0
Aug.	1.8	9.9	11.1	27.8	12.6	1.6	1.2
Sep.	3.8	3.9	4.0	12.2	4.1	2.7	0
Oct.	1.1	0.9	1.3	5.0	5.0	2.3	0
Nov.	0	0.2	0	0.4	0	0.1	0
Dec.	0	0	0.1	0.5	0.1	0.5	0

Polydactylus octonemus in the demersal phase have an apparent total annual mortality rate off Texas that approaches 100%, mean time- and cohort-specific values being 97–100%. Only one winter cohort was present in 31 of 32 months off Freeport (Fig. 6), so time-specific estimates were 100% in each of these instances. Cohort-specific values were 100% in 6 of 7 months for 1978, 8 of 8 months for 1979, and 5 of 5 months for 1980 fish because N_t was zero. A time-specific estimate for April 1979 and a cohort-specific estimate for the 1978 cohort in April of 1978 and 1979 were 75% and 95% ($Z = 1.39$ and 3.00), respectively, but the former value may be an underestimate because the younger cohort was incompletely recruited in April.

Table 3

Mean total length (mm) for *Polydactylus octonemus* in Galveston Bay, 1968 and 1969 (adapted from Gallaway and Strawn 1974), and by depth in the Gulf off Freeport, Texas. Data at each depth in the Gulf are for age-0 fish pooled over the period October 1977–August 1981.

	Galveston Bay		Gulf of Mexico (depth in m)							
Month	1968	1969	5	9	13	16	18	22–24	27	86
Mar.			74.0							
Apr.	77.2	65.7	70.7	80.5						75.0
May	78.3	81.6	84.9	86.7	76.9	80.7				
June	86.6	92.7	109.4	127.1	132.1	123.2	139.2	147.7	164.0	
July	93.1	117.5	133.6	148.6	142.8	156.4	163.5	157.0		
Aug.	102.3	129.5	140.6	157.1	159.9	164.5	173.4	165.5	164.9	
Sep.	109.7	132.0	168.2	169.4	168.5	164.7	168.8	175.7		
Oct.	114.1	140.3	163.0	160.1	167.2	165.0	173.6	185.5		
Nov.	104.8					194.7		189.7		
Dec.	123.9				164.0	185.9	186.0	181.8		
Jan.	158.0									

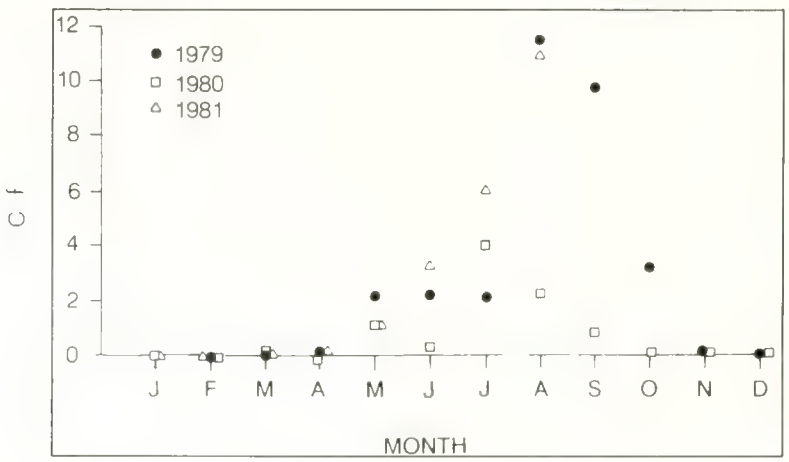


Figure 12

Catch/effort (mean number/10-min tow) by month of *Polydactylus octonemus* off Freeport, Texas, each year.

Table 4

Observed mean sizes (mm TL), size ranges, and predicted sizes by hatching-date regressions (Fig. 2) and von Bertalanffy models for 1977–80 *Polydactylus octonemus* cohorts at 6, 9, and 12 months of age. Observed values are pooled data from July–August at 6 months and October–November at 9 months. Dentzau (1985, table 4) gives more detail.

	Observed sizes			
	6 mo		9 mo	
Year	Mean	Size range	Mean	Size range
1977	–	–	178	144–200
1978	153	125–176	178	160–214
1979	154	107–194	183	157–212
1980	148	86–197	207	194–214
1981	160	103–223	–	–

	Predicted sizes					
	6 mo		9 mo		12 mo	
	Regression	von Bertalanffy	Regression	von Bertalanffy	Regression	von Bertalanffy
1978	133	136	172	166	192	181
1979	163	157	186	187	–	205
1980	141	–	212	–	–	–

Table 5

Total weight–total length, girth–total length, and length–length regressions for *Polydactylus octonemus* with supporting statistics. All regressions were significant at $\alpha = 0.05$. The symbol v is from Ricker's (1973) GM regression. Measures are grams and millimeters. See Methods for symbols.

Equation	n	Range	$100\,r^2$	v
Log_{10} TW = −5.72 + 3.27 Log_{10} TL (males + females + immatures)	2398	51–226	99.0	3.29
Log_{10} TW = −6.29 + 3.53 Log_{10} TL (males + females)	800	107–226	94.2	3.64
Log_{10} TW = −6.50 + 3.63 Log_{10} TL (males)	286	126–207	92.8	3.76
Log_{10} TW = −6.25 + 3.51 Log_{10} TL (females)	514	107–226	94.8	3.60
TL = 15.10 + 1.70 G	847	51–226	94.8	1.74
G = −4.22 + 0.56 TL	847	51–226	94.8	0.57
TL = −1.04 + 1.42 SL	847	51–226	99.1	1.43
SL = 1.74 + 0.70 TL	847	51–226	99.1	0.70
TL = −2.77 + 1.26 FL	2398	51–226	99.5	1.27
FL = 2.80 + 0.79 TL	2398	51–226	99.5	0.79

Weight, girth, and length relationships

Total weight–total length regressions for males and females (Table 5) were not significantly different in slope ($F = 2.91$, df = 1, 798), but they differed in elevation ($F = 7.73$, df = 1, 799). Therefore, equations are presented for each sex and for males and females pooled. Total weight–total length regressions for all fish and for males and females pooled were significantly different in slope ($F = 99.10$, df = 1, 2056); however, the one equation that pools all fish may be useful at this stage of management.

Discussion

Spawning periodicity

The primary winter–spring spawning period we found for *Polydactylus octonemus* in the northwestern Gulf,

Table 6

Available information on larval, young (see text footnotes 1 and 4), and juvenile specimens of *Polydactylus octonemus* collected in western Gulf of Mexico surface waters by plankton net, dip net, meter net, and neuston net. Reference numbers correspond to locations in Figure 13.

Reference number	Location collected (lat.°N)	Location collected (long.°W)	Collection date	Depth (m)	Length (mm)	Reference
			Texas and Louisiana			
1	Gulf off Barataria Bay, Louisiana		Apr. 33	<22	50 TL	Gunter 1938b
2	26°40′	92°00′	8 May 54	1602	–	Springer and Bullis 1956
3	26°05′	95°25′	27 May 54	1890	–	Springer and Bullis 1956
4	26°15′	95°00′	7 Mar. 65	≅2300	44–54 TL	Pequegnat (text footnote 3)
5	27°52′	93°48′	Mar. 72	137	57–71 TL	Bright and Cashman 1974
6	27°33′	96°06′	Jan.–Feb. 76	134	35–36 TL	Pequegnat et al. 1977
7	26°57′	96°32′	Jan.–Feb. 76	106	38–47 TL	Pequegnat et al. 1977
8	26°10′	96°24′	27 Feb. 76	91	21–52 TL	Pequegnat et al. 1977
9	27°17′	96°23′	25 Mar. 76	131	40 TL	Pequegnat et al. 1977
10	27°30′	96°44′	8 Apr. 76	49	56 TL	Pequegnat et al. 1977
11	27°17′	96°23′	10 Apr. 76	131	43–80 TL	Pequegnat et al. 1977
12	26°58′	97°11′	29 May–8 June 76	25	–	Pequegnat et al. 1977
13	27°17′	96°23′	20 Apr. 77	131	65–72 TL	Wormuth et al. 1979
14	27°34′	96°07′	15–21 May 77	134	–	Wormuth et al. 1979
15	26°10′	96°24′	15–21 May 77	91	–	Wormuth et al. 1979
16	Gulf off Freeport		6 May 79	54	56–66 TL	Rockett[1]
17	28°14′	94°57′	23 Apr. 59	47	–	Bullis and Thompson 1965
18	26°00′	96°00′	22 Apr. 82	200	44 SL	Lieby[2]
19	26°30′	94°30′	24 Apr. 82	200	39–51 SL	Lieby
20	27°00′	92°00′	25 Apr. 82	200	40–48 SL	Lieby
21	27°30′	92°30′	10 May 82	200	41–44 SL	Lieby
22	27°30′	93°30′	10 May 82	200	45 SL	Lieby
23	28°00′	94°00′	9 May 82	58	38–45 SL	Lieby
			Mexico			
24	20°01′	92°27′	14 May 54	1467	–	Springer and Bullis 1956
25	19°13′	95°34′	17 May 54	1260	–	Springer and Bullis 1956
26	20°34′	95°37′	20 May 54	2160	–	Springer and Bullis 1956
27	21°42′	93°35′	22 May 54	2736	–	Springer and Bullis 1956
28	24°00′	96°50′	25 May 54	1035	–	Springer and Bullis 1956
29	24°54′	96°05′	27 May 54	1530	–	Springer and Bullis 1956
30	25°08′	94°58′	9 Mar. 65		48 TL	Pequegnat (text footnote 3)
31	23°14′	96°08′	23 Apr. 75		49–60 TL	Kennicutt (text footnote 3)
32	23°00′	96°52′	24 Apr. 75	–	53–66 TL	Kennicutt (text footnote 3)
33	20°40′	92°55′	25 Nov. 56	2088	–	Bullis and Thompson 1965
34	20°40′	96°05′	2 Apr. 56	1782	–	Bullis and Thompson 1965
35	19°35′	95°28′	11 Apr. 56	2300	–	Bullis and Thompson 1965

[1]M. Rockett, Appalachian State Univ., Boone, NC 28608, pers. commun., March 1981.
[2]M. Lieby, Bur. Mar. Res., St. Petersburg, FL 33701, pers. commun., Feb. 1986.

mid-December–mid-March and continuing at a lower level through April or May, generally agrees with the limited literature. Gunter (1938b, 1945) suggested fall–winter or late winter–early spring spawning, because 28–100 mm young appeared from April through June. Winter–spring spawning is also supported by: (1) collection of neustonic "larvae"[1] 21–80 mm[2] in water 25–134 m deep over the south Texas continental shelf primarily from mid-January through early April, but also into early June (Pequegnat et al. 1977); (2) collection at the surface of fish (a) 44–54 mm in water 2300 m deep in early March off south Texas (26°15′N, 95°00′W)[3], (b) 57–71 mm (41–51 mm SL) in water 137

[1]Larvae as used by Pequegnat et al. (1977) and Wormuth et al. (1979) may encompass the juvenile stage defined by Moyle and Cech (1982).
[2]We obtained sizes from specimens deposited at the Texas Cooperative Wildlife Collection (TCWC), Texas A&M University, College Station, TX.
[3]Fish were collected by W. Pequegnat and M. Kennicutt (Dep. Oceanogr., Texas A&M Univ.), and deposited in TCWC.

m deep in March over the West Flower Garden Bank off Texas (27°52′N, 93°48′W; Bright and Cashman 1974), (c) 50 mm in water <22 m in April off Barataria Bay, LA (Gunter 1938b), and (d) 56–66 mm in water 54 m deep in early May off Freeport (M. Rockett, Appalachian State Univ., Boone, NC 28608, pers. commun., March 1981); (3) collection at the surface in early May of "young"[4] off south Texas (26°05′N, 95°25′W) and off the Louisiana continental shelf (26°40′N, 92°00′W) in water 1890 and 1602 m deep, respectively (Table 6; Springer and Bullis 1956); and (4) collection of neustonic "larvae" (footnote 1) 65–72 mm in water 91–134 m deep in mid-April–mid-May off south Texas (Wormuth et al. 1979).

Our calculated spawning-period duration of 45–120 days assumes large fish hatch before small ones and all grow at the same rate (Geoghegan and Chittenden 1982). The latter assumption appears reasonable, because 99% confidence intervals for observations (in Dentzau 1985, table 3) were fairly constant between cruises within each May–June period. Our calculated duration may be an overestimate because continued recruitment of small fish to the Gulf would tend to depress estimates of mean growth/day, the denominator in our spawning-duration equation. The numerator, mean size range, is less affected; larger recruits gradually disperse offshore to deeper waters, but we collected throughout and beyond the bathymetric range of the species. Comparisons of spawning-period durations from 90 and 99% confidence intervals are valid, however; such calculations use the same values except t.

Our calculated hatching dates indicate mid-January–mid-February spawning, these being mean spawning dates because regression predicts averages. They are in error to the extent that regression curves do not pass through the origin and that they are asymptotic to the x- or y-axis in very early life. The latter is an unknown; the former problem does not seem serious, because Shirota (1970, in Hunter 1981) found length at first feeding in many species is four times the egg diameter. Egg diameter is not known in *P. octonemus* (Martin and Drewry 1978, deSylva 1984), but it averages 0.76 mm in the closely related *Eleutheronema tetradactylum* (deSylva 1984). This suggests *P. octonemus* is 3–3.5 mm at hatching, so only a few days error occurs in x, at most.

Spawning areas

Any spawning of *P. octonemus* in the northern or northwestern Gulf presumably occurs in the water column. Our data and the literature (Chittenden and McEachran 1976; Wohlschlag et al. 1977, 1979) indicate they basically disappear as demersal fish from the white and brown shrimp communities of the northern Gulf in November–December. They may assume a pelagic behavior then, which would explain their apparent absence in January–February, because Hastings et al. (1976) observed this species in December in habitat typical of pelagic fish—open water areas around an offshore platform in water 18 m deep in the northeastern Gulf off Panama City, Florida.

Catch records for young in the literature and the disappearance of *P. octonemus* from the white and brown shrimp communities in their primary winter spawning period, if the latter does not simply reflect gear selectivity following assumption of a pelagic habit, suggest this species spawns along the outer continental shelf, the continental slope, or further offshore. Although pelagic "larvae" (footnote 1) and juveniles have been collected at the surface in or near waters of the white shrimp community off Texas and Louisiana in April–early June (collections 1 and 12, Fig. 13) or the brown shrimp community in late February–May (collections 8, 10, 15, 16, and 23, Fig. 13), more frequent collections in U.S. waters have been made along the outer continental shelf at 106–137 m in January–May (collections 5, 6, 7, 9, 11, 13, and 14, Fig. 13), and even further offshore at ≥200–2300 m in March-May (collections 2, 3, 4, 18, 19, 20, 21, and 22, Fig. 13). Several collections of "young" (footnote 4) and juveniles have been made in Mexican waters 1035–2736 m deep between Laguna Madre Tamaulipas and Campeche Bank in March–May (collections 24–32, Fig. 13). Similarly, young of other *Polydactylus* spp. also occur off continental shelves although adults are common in inshore waters; e.g., Klawe and Alverson (1964) found young *P. opercularis* and *P. approximans* <48 mm 250 nm offshore in the eastern tropical Pacific Ocean.

In contrast to the abundance of *P. octonemus* larvae and juveniles in the western and northwestern Gulf, they have not been identified in extensive collections off the west coast of Florida from Pensacola on the north, south to the Florida Keys (Vick 1964; Houde et al. 1979; M. Lieby, Bur. Mar. Res., St. Petersburg, FL 33701, pers. commun., Feb. 1986). This suggests little or no spawning in that area and in the eastern side of the Loop Current, which contributes water to the western Florida shelf (Austin and Jones 1974).

Polydactylus octonemus eggs, larvae, and juveniles, pelagic like other polynemids (Breder and Rosen 1966, Kagawade 1970), presumably use current transport to reach their estuarine and shallow Gulf nurseries. Standard and Chittenden (1984), based on Murphy and Chittenden (unpubl.), suggested spawning in *Larimus fasciatus* and other Gulf fishes is timed to coincide with

[4]Springer and Bullis (1956) defined young as postlarval, juvenile, and young specimens.

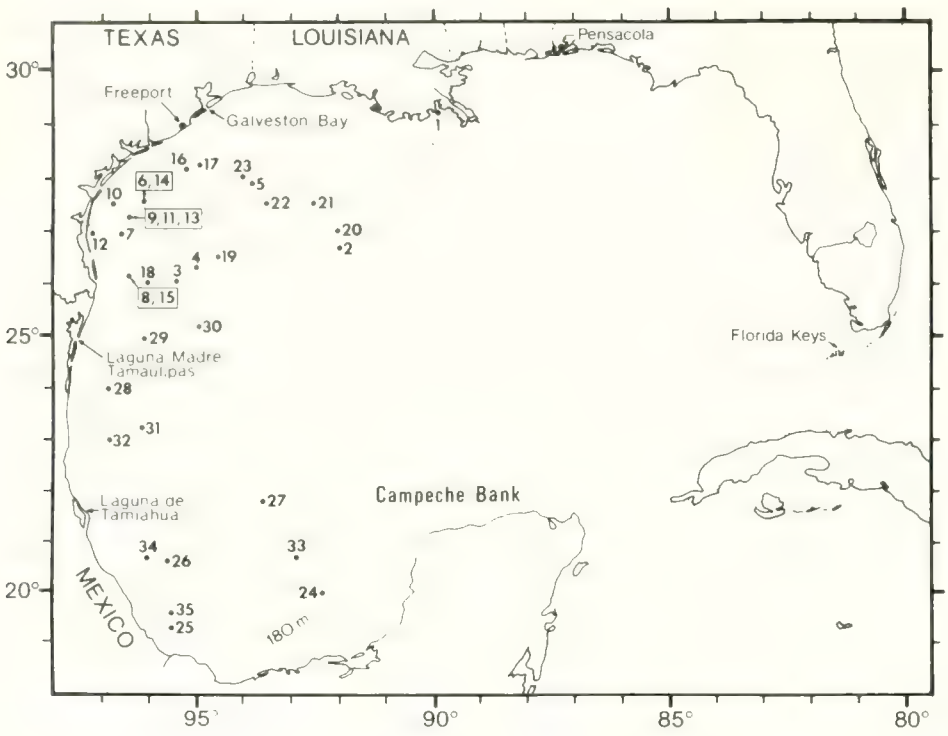


Figure 13
Summary of available collections of larval, young (see text foonotes 1 and 4, and juvenile *Polydactylus octonemus* from surface waters in the Gulf of Mexico. Reference numbers correspond to those in Table 7 where collection information is given.

the occurrence of downcoast alongshore coastal currents (towards Mexico) and onshore surface Ekman transport caused by downcoast wind stress along much of the Texas and western Louisiana coast from August–September through April–May (Kelly et al. 1981). When alongshore currents are downcoast, an eastward or northeastward counterflow along the shelf break forms a cyclonic gyre on the continental shelf off Texas and western Louisiana (Kelly et al. 1984). The alongshore components of this gyre probably transport, in merry-go-round fashion, eggs, larvae, and juvenile *P. octonemus* from the outer shelf and slope to their shallow nurseries. Portions of this current not diverted westward at the Mississippi Delta (Kelly et al. 1983) may carry eggs and larvae east towards the west coast of Florida where older stages of *P. octonemus* have been collected in the surf and estuaries (Powell et al. 1972, Ogren and Brusher 1977) even though, as noted, larvae have not been found. Shaw et al. (1985) suggested a similar model for Gulf menhaden *Brevoortia patronus*.

Onshore surface Ekman transport components of the gyre seemingly could transport young *P. octonemus* directly inshore in the northwestern Gulf; however, this does not seem to be the case. Unlike *P. octonemus*, fishes of the brown shrimp community which spawn offshore and have pelagic eggs and larvae do not appear to be transported into the white shrimp community; they are basically absent there (Chittenden and McEachran 1976).

Depending on how long the young remain pelagic, current regimes are such that the spawning areas that produce young *P. octonemus* of the northwestern Gulf can lie almost anywhere in the western or central Gulf. Recent studies (Parker et al. 1979) cited in Rezak et al. (1983) found almost all surface drifters released west of a line from the Mississippi delta to the middle of the Yucatan Straits washed ashore along Texas; those released to the east were almost all found outside the Gulf along the Atlantic coast of Florida. This probably reflects a well-documented picture of Gulf circulation (Nowlin and McLellan 1967, Nowlin 1972, Behringer et al. 1977, Merrell and Morrison 1981, Merrell and Vasquez 1983): The major driving force for nearsurface circulation in the deep eastern Gulf is the Loop Current which enters the Gulf via the Yucatan Straits, loops toward Alabama, and turns back to exit the Gulf via the Florida Straits. The major driving force in the western Gulf is a large, permanent anticyclonic gyre, centered at 23.5°N, and maintained by consistent pinching off and westward drift of Loop Current rings (Merrell and Morrison 1981) or wind stress curl across the western Gulf (Sturges and Blaha 1976, Merrell and Vasquez 1983). South of this gyre is a cyclonic gyre in the Bay of Campeche from which water joins a predominantly northerly flow along the Mexican shelf (Nowlin 1972, Merrell and Morrison 1981, Rezak et al. 1983). Pelagic early stages of *P. octonemus* have been collected along much of the western Gulf margin (Fig. 13). The northerly flow there could transport pelagic

young towards Texas. The coastal area off south Texas and northern Mexico has converging currents much of the year, water which at least in part heads easterly or northerly along the shelf edge after leaving the coast near 26°N. Whatever their source, pelagic young transported to and entrained in the gyre of the Texas–western Louisiana shelf could be transported to inshore and estuarine nurseries there.

Bathymetric distribution, recruitment, and movements

Our finding that *P. octonemus* is most abundant at depths ≤22 m in the northwestern Gulf agrees with Hildebrand (1954) and Chittenden and McEachran (1976), who only captured it in the demersal phase and considered it a member of the white shrimp community. Maximum depths recorded for the demersal form of this species in the Gulf are 66 m off Louisiana (Springer and Bullis 1956) and 65 m off Texas (Wohlschlag et al. 1979).

Our finding that *P. octonemus* appears late March–April and basically disappears late October–late December agrees with the literature for Texas and Louisiana including Gunter (1938b, 1945), Perret et al. (1971), and Gallaway and Strawn (1974). Some reports indicate a few fish occur in winter in the white and brown shrimp communities throughout the northern Gulf: (1) in January in Galveston Bay, Texas (Gallaway and Strawn 1974, Sheridan 1983), (2) at 18–22 m in January off Texas (Chittenden and McEachran 1976), (3) in shallow waters in January and February at Sabine Lake and Holly Beach, Louisiana (Perry and Carter 1979), and (4) at 40 m in early February off Alabama (Bullis and Thompson 1965). The similar periodicity of reported occurrence suggests similar movements and spawning periodicity throughout the northwestern and north-central Gulf.

The spring recruitment we found in *P. octonemus* agrees with data in several studies from the northern Gulf including Gunter (1945) and Miller (1965) in Texas, Gunter (1938b) and Perret et al. (1971) in Louisiana, and Ogren and Brusher (1977) in northwestern Florida. Recruitment appears concurrent in estuaries and the shallow Gulf, because we collected fish 50–105 mm in the Gulf off Texas at ≤9 m in April, the same period when Gallaway and Strawn (1974) and Landry (1977) collected fish in Galveston Bay 56–97 mm (40–69 mm SL) and 74–101 mm (53–72 mm SL), respectively. Moreover, demersal phase fish first appeared the same month in both Barataria Bay and the shallow Gulf off Louisiana (Gunter 1938b).

Our finding that *P. octonemus* disperse offshore beginning in early summer agrees with the literature. Gunter (1945), Gallaway and Strawn (1974), and Perret et al. (1971) found abundance declined in estuaries in June–August or September, at about the same time (July–September) we found greatest abundance in the Gulf and size gradients from estuaries to offshore. We found the largest, oldest fish in the deeper areas of the white shrimp community or in the transition community (Chittenden et al. 1982) as they dispersed offshore. This pattern has also been suggested for other species of the Gulf white shrimp community such as *Micropogonias undulatus*, *Peprilus burti*, *Cynoscion arenarius*, and *Larimus fasciatus* (White and Chittenden 1977, Murphy 1981, Shlossman and Chittenden 1981, Standard and Chittenden 1984).

Age determination and growth

Age determination, size at age, and von Bertalanffy parameters have not been previously described for *P. octonemus*. Our calculations for growth are based on sizes at known time scaled to calculated hatching dates to give age. Regression coefficients and K values are the same regardless of hatching date, however, because curves are fitted to the same time dimension between the first and last collections of a cohort.

We determined age in months and years by length-frequency analysis because we had almost 4 years of data from cruises so close in time that modes were easily followed, and only one cohort usually occurred at a given time. As in *Stenotomus caprinus* (Geoghegan and Chittenden 1982) and *Larimus fasciatus* (Standard and Chittenden 1984), modal-group progression analysis can be a superior method of age determination in *P. octonemus* because (1) spawning primarily occurs in one discrete period, (2) growth of large and small fish in a cohort appears uniform because variances were generally constant between cruises, (3) length frequencies are reasonably normally distributed within cohorts, and (4) age need only be determined for 1 or 2 years, ideal conditions for using length frequencies (Lagler 1956, Bagenal and Tesch 1978).

Although it would be desirable to support our aging findings by the more time-consuming analysis of daily otolith increments (Jones 1986), the growth and other parameters we present provide useful upper or lower boundaries for true values (see comments in Methods). We reiterate that our sizes at age and von Bertalanffy parameters are apparent ones; they are affected to an unknown degree by a combination of recruitment, and, especially as the fish approach age I, emigration, gear avoidance, and change from demersal to pelagic behavior. Because of similar problems, Knudsen and Herke (1978) suggested length frequencies should not be used to estimate growth in *Micropogonius undulatus*. We do not agree, however, because the fundamental problem is not the length-frequency method. Rather, it is

how best to draw a random sample in time and space to characterize the population. The time dimension has three major aspects of variation (diel, annual, and monthly or seasonal), as does the spatial (along-shelf, across-shelf and estuary, and vertical). No published Gulf study to our knowledge addressed all six aspects, and few addressed any to the extent we did. Our design directly addressed all three time aspects and the across-shelf spatial dimension. We addressed along-shelf and estuarine variation indirectly by referencing the considerable literature. We were not able to address vertical variation, but apparently no published work has done that. The problem of getting representative data for *P. octonemus*—indeed, for many other Gulf species—may not be fully solved till all six aspects of sampling are concurrently addressed in one study.

Maximum size, life span, and mortality

The largest *P. octonemus* we collected in the northwestern Gulf (229 mm) is very close to that reported from off Virginia (233 and 235 mm ?L, Hildebrand and Schroeder 1928), the only Atlantic coast location with published sizes. Breder (1948) noted this species reaches one foot in length but gave no details to support the figure; it is only 2–3 inches larger than our maximum sizes and might reflect a rough rounding-off by him. The largest *P. octonemus* we found is slightly larger than maximum sizes in other Gulf studies [off Texas: 213 mm (Gunter 1945), 210 mm (Compton and Bradley 1963), 213 mm (171 mm FL) (Chittenden and McEachran 1976); Off Mississippi: 197 mm (Christmas and Waller 1973); Off Florida: 209 mm ?L (Powell et al. 1972)]. However, these reported maximum lengths are similar to the apparent typical maximum size of 202–206 mm we found. Smaller maximum sizes in other Gulf reports such as Gunter (1938b), Perret et al. (1971), Gallaway and Strawn (1974), and Perry and Carter (1979) may reflect gear selectivity or the fact they collected largely in estuaries, surf, and shallow Gulf areas. The studies cited, however, took place over much of the northern Gulf so the demersal stage of *P. octonemus* appears to show little, if any, east-west spatial variation in maximum sizes.

Our finding the largest, oldest *P. octonemus* in the deeper areas of the white shrimp community may reflect a broad life-history pattern for species there, many of which show a positive size gradient towards offshore. This has been reported for strongly estuarine dependent species such as *Micropogonius undulatus* and *Cynoscion arenarius* (White and Chittenden 1977, Shlossman and Chittenden 1981), and more marine forms such as *Peprilus burti* and *Larimus fasciatus* (Murphy 1981, Standard and Chittenden 1984).

The apparent typical maximum life span of 1 year we found for *P. octonemus* in the northwestern Gulf agrees with Chittenden and McEachran (1976) and appears reasonable, at least for the demersal stage, because the maximum and typical maximum sizes we observed are similar to, or larger than, all other values reported for the Gulf. The value of $t_L = 1$ year might be a little low because *P. octonemus* disappears at 9–11 months of age to spawn in winter, and because we collected one fish 15 months of age in April. That one fish is the only instance in 71 cruises in which a second year class co-occurred with young-of-the-year, so our data clearly indicate that at least the demersal phase of life basically ends at 1 year. Though the literature indicates no east-west spatial variation in maximum size, and age by inference, *P. octonemus* might survive their first spawning and assume a pelagic behavior. Bullis (1961) observed a dense ball of small *Polydactylus* sp., which could have been young or adult *P. octonemus*, *P. virginicus*, or *P. oligodon* (Fischer 1978), at the surface along the 500-fm curve in August in the western Caribbean.

Midwater and surface collections are needed to resolve the duration of a pelagic phase in adult *P. octonemus*; that would clarify the validity of the several life-history parameter values we have termed "apparent." In addition, collections with trawls larger than we and other workers have used would clarify if and how gear-avoidance affects parameter values. Despite these possible problems, however, it seems clear that few adult *P. octonemus* resume a demersal existence in the white or brown shrimp communities after age I. We collected only one fish older than 12 months, and Chittenden and McEachran (1976) caught no fish older than 12 months even though they caught 33 specimens on the white shrimp grounds in January.

The apparent mean time- and cohort-specific total annual mortality rates we observed for *P. octonemus* (97–100%) agree with theoretical estimates of 90–100% (Royce 1972:238) if maximum life span is typically only 1–2 years. Though these are also apparent values, they are not that far from the range of values for another well-studied, exploited pelagic species, *Brevoortia patronus*. In that species, total annual mortality rate is 83–95% depending on age (Nelson and Ahrenholz 1986). Moreover, the population dynamics of *P. octonemus* in the northwestern Gulf appear generally similar to those reported for many other species there including *Micropogonius undulatus* (White and Chittenden 1977), *Cynoscion arenarius* (Shlossman and Chittenden 1981), *Cynoscion nothus* (DeVries and Chittenden 1982), *Peprilus burti* (Murphy 1981), *Stenotomus caprinus* (Geoghegan and Chittenden 1982), *Larimus fasciatus* (Standard and Chittenden 1984), and *Leiostomus xanthurus* (Hata 1985). This similar-

ity over a variety of species supports the suggestions (Chittenden and McEachran 1976, Chittenden 1977) that fishes of the white and brown shrimp communities, at least in the northwestern Gulf, have evolved a common pattern of population dynamics which stresses small size, early maturity, short life spans, high mortality rates, and rapid turnover of biomass.

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Abstract.—The feeding habits of late-larval and early-juvenile walleye pollock *Theragra chalcogramma* from a coastal nursery habitat in the western Gulf of Alaska were examined in relation to fish size (10.0–29.9 mm SL) and site of collection. *Pseudocalanus* sp. was the dominant prey. Copepod nauplii and *Pseudocalanus* copepodids decreased in importance in the diet as fish size increased, concomitant with an increase in importance of adult *Pseudocalanus* sp. and *Calanus* spp. Other prey showed no clear relation to fish size. A comparison of diet between collection stations revealed considerable variability. Along two transects perpendicular to the Alaska Peninsula, between-station diet overlap was observed to be high for one transect, and low for the other. Along a transect parallel to the Alaska Peninsula, some adjacent stations yielded high diet overlap, and other yielded low overlap, while the most distant stations produced high diet overlap. Patchiness of food resources likely contributed subtantially to these patterns. One possible consequence of the ingestion of different prey in different locales is that differential growth rates could result.

Feeding Ecology of Late-Larval and Early-Juvenile Walleye Pollock *Theragra chalcogramma* from the Gulf of Alaska in 1987*

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The recent discovery of large spawning aggregations of walleye pollock *Theragra chalcogramma* in Shelikof Strait from late March to mid-April suggests that this is the principal spawning center for the species in the Gulf of Alaska (Dunn et al. 1984, Kendall et al. 1987). The concentrated mass of eggs produced in Shelikof Strait in early spring and the ensuing dense patch of larvae provide uncommon access to the early life history of the species. The spawning aggregations produce distinct cohort patches (20 × 50 km or larger) of eggs at depths greater than 150 m (Incze et al. 1989). After about 14 days, the eggs hatch (Dunn and Matarese 1987, Kim 1989) and larvae ascend to the upper 50 m (Incze et al. 1989). The larval patches can be followed for up to 30 days as they drift with prevailing currents to the southwest (Kendall et al. 1987, Hinckley et al. 1989, Incze et al. 1989). The cohesiveness of the patches likely results from the restricted spawning area within Shelikof Strait (Hinckley et al. 1989) as well as Alaska Coastal Current circulation patterns (Incze et al. 1989).

Ichthyoplankton has been surveyed regularly in and around Shelikof Strait since 1979, and much is known regarding the early life history of walleye pollock in this area (e.g., Kendall et all 1987, Incze et al. 1989, Kim 1989, Yoklavich and Bailey 1989). However, considerably less is known about life history of late-larval and juvenile stages within nursery habitats in the western Gulf of Alaska. A survey in June and July 1987 collected late-larval and early-juvenile pollock from a coastal nursery area over the continental shelf along the Alaska Peninsula (Hinckley et al. 1989). While the center of distribution was between the Shumagin and Semidi Islands, a large number of late larvae and juveniles were collected over a broad area running nearly the length of the Alaska Peninsula. The broad distribution enabled us to examine whether diet varied along the length of the Alaska Peninsula and along a nearshore-offshore transect. Although the feeding habits of the late larvae have been previously reported from several locations, in all cases results have been pooled across collection stations (Kamba 1977, Clarke 1978, Cooney et al. 1980, Lee 1985, Kendall et al. 1987). In the present study, feeding habits of late larvae were analyzed by size and these data are compared to previous reports. Further, diet was analyzed by collection station, and between-station differences were examined using a measure of diet overlap.

Materials and methods

Pollock larvae were collected in the Gulf of Alaska during June 1987 by the RV *Miller Freeman*. Collections were made using a 5-m^2 Methot frame trawl (Methot 1986) (2 × 3 mm oval mesh) that was fished obliquely

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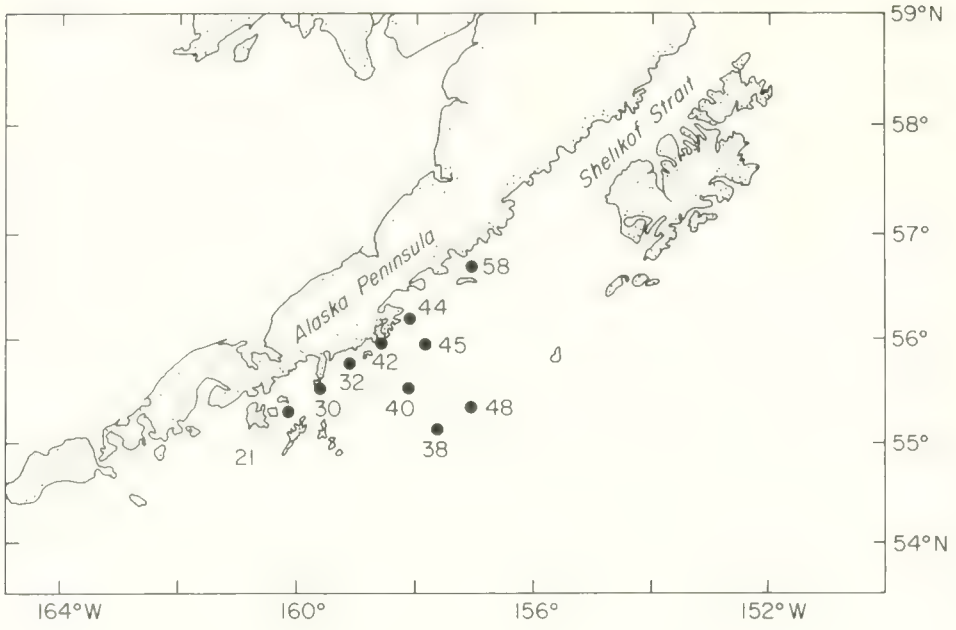

Figure 1
Location of collection stations in the Gulf of Alaska. Stations represent one transect parallel to the Alaska peninsula, and two perpendicular offshore transects, with stations 38 and 48 located near the shelf break.

from 15 m off-bottom (to a maximum of 300 m depth) to the surface (Hinckley et al. 1989). Samples from 10 stations, representing 2 nearshore-offshire transects (stations 38, 40, and 42 and stations 44, 45, and 48) and one transect parallel to the Alaska Peninsula (stations 21, 30, 32, 42, 44, and 58; see Figure 1), that were collected from 20 to 25 June, were the focus of this study. The total number of fish examined was 490.

Samples were preserved in 5% formalin at sea, and transferred to 70% ethanol prior to their examination. Specimen shrinkage most likely occurred as a result of fixation.

After the standard length (SL) of each larva was measured, the digestive tract was removed. Contents of the entire digestive tract were evaluated. Gut contents were teased out and prey items were identified: invertebrate eggs, copepod nauplii, barnacle nauplii, euphausiid larvae, pteropods, other non-copepod prey, and copepods including *Pseudocalanus* sp. adults (CVI), *Pseudocalanus* copepodids (CI–CV), *Acartia longiremis*, *Acartia* sp., *Calanus marshallae*, *Calanus* sp., *Centropages abdominalis*, *Eucalanus bungii*, *Metridia* sp., *Oithona* sp., *Oncaea* sp., unidentified calanoid copepodids <1.5 mm, and unidentified calanoid copepodids >1.5 mm. Copepod eggs comprised over 99% of the "invertebrate eggs" category and *Oithona similis* comprised over 99% of the "*Oithona* sp." category. While the taxonomy of the genus *Pseudocalanus* has recently been clarified (Frost 1989), no attempt at specific identifications of *Pseudocalanus* was made in the present study. For all copepods except *Pseudocalanus* sp., copepodid (CI–CV) through adult stages were considered together. Copepodids were inconsequential in all species except *Calanus* sp.

Diet was analyzed in terms of numerical percentage composition (%N), volumetric percentage composition (%VOL), and percent frequency of occurrence (%FO). Prey volumes were estimated using prey dimensions (Grover and Olla 1987). Over 8000 prey items were measured for prey volume calculations. The three analyses (%N, %VOL, and %FO) were combined to yield a more comprehensive assessment of prey importance, the index of relative importance ($IRI = (\%N + \%VOL) \times \%FO$) (Pinkas et al. 1971). Data were pooled across stations for analysis by size class. The four size classes were defined as 10.0–14.9, 15.0–19.9, 20.0–24.9, and 25.0–29.9 mm SL. For station-by-station analyses, data were pooled across size classes.

Diet overlap was calculated using an index of proportional similarity (Wallace 1981, Linton et al. 1981, Kohn and Riggs 1982) defined as

$$PS = 1 - 0.5 \left(\sum_{i=1}^{n} \left| P_{xi} - P_{yi} \right| \right)$$

where PS is the index of proportional similarity or overlap, P_{xi} is the proportion of prey category i in the diet at location x, P_{yi} is the proportion of prey category i in the diet at location y, and n is the number of prey categories. Mean percent volume was used as a measure of diet for these calculations (Wallace 1981). Although this index has been traditionally used to examine diet overlap between species at one location, I have used it to examine diet overlap between locations for

Table 1
Mean lengths of late-larval and early-juvenile walleye pollock collected at 10 stations in the Gulf of Alaska in 1987 (with standard deviations), and date and time of collection.

Station no.	Standard length (mm)	Collection Date	Collection Time (h)
21	16.1 (2.11)	20 June	2156
30	18.2 (2.27)	22 June	0144
32	17.4 (1.74)	22 June	0704
38	19.3 (3.27)	22 June	2205
40	18.6 (2.06)	23 June	0114
42	18.4 (2.44)	23 June	0558
44	17.1 (2.47)	24 June	1756
45	19.9 (2.40)	24 June	1956
48	20.2 (2.55)	25 June	0117
58	19.0 (3.36)	25 June	2314

a single species. This index was chosen because it does not require resource-availability data (Wallace 1981), it is independent of sample size (Kohn and Riggs 1982), and it estimates overlap accurately for real overlaps between 7 and 85%, whereas three other indices performed poorly (Linton et al. 1981). *PS* values greater than 60% are generally considered to demonstrate significant overlap (Mathur 1977, Wallace and Ramsey 1983). In order to minimize size-related bias in the measurement of diet overlap, proportional similarity indices were calculated for only the 15.0–19.9 mm SL size class.

Results

Standard length tended to increase with date of collection (Table 1, correlation coefficient $r = 0.678$, $P < 0.05$). The dominant size class for all stations was 15.0–19.9 mm SL, accounting for 62% of the larvae, with a minimum of 21 larvae of this size collected at each station. The mean lengths of larvae from five stations located along a transect parallel to the Alaska Peninsula were significantly different ($P<0.001$) (ANOVA, Zar 1974), while of the two transects perpendicular to the Alaska Peninsula, larval lengths were significantly different ($P<0.001$) along only one of these transects (stations 44, 45, and 48).

Table 2
Diet of walleye pollock from the Gulf of Alaska in 1987, by size class, expressed as *%N*, *%VOL*, *%FO*, and *%IRI*.

	10.0–14.9 mm SL ($N=50$)				15.0–19.9 mm SL ($N=302$)				20.0–24.9 mm SL ($N=127$)				25.0–29.9 mm SL ($N=7$)			
	%N	*%VOL*	*%FO*	*%IRI*	*%N*	*%VOL*	*%FO*	*%IRI*	*%N*	*%VOL*	*%FO*	*%IRI*	*%N*	*%VOL*	*%FO*	*%IRI*
Invertebrate eggs	15.8	0.8	66.0	7.3	25.8	0.9	62.6	12.4	27.1	0.6	67.7	13.3	15.9	0.3	42.9	4.7
Copepod nauplii	25.3	2.8	86.0	16.1	9.3	0.7	63.2	4.7	1.5	0.1	40.9	0.5	0.5	<0.1	14.3	<0.1
Barnacle nauplii					0.1	<0.1	4.3	<0.1	0.1	<0.1	4.7	<0.1				
Euphausiids	1.1	6.4	24.0	1.2	0.8	3.0	20.5	0.6	0.7	1.9	20.5	0.4	0.7	1.3	28.6	0.4
Pteropods	0.6	0.3	8.0	<0.1	1.6	0.5	16.9	0.3	0.4	0.1	6.3	<0.1				
Other					0.2	0.1	5.3	<0.1	<0.1	<0.1	3.1	<0.1				
Pseudocalanus sp.	8.8	30.7	82.0	21.6	14.6	35.5	79.5	29.5	26.6	43.1	87.4	43.3	37.2	40.7	100.0	52.9
Pseudocalanus copepodids	6.7	9.1	76.0	8.0	7.5	7.2	66.6	7.3	7.8	5.0	69.3	6.3	8.6	3.7	57.1	4.8
Acartia longiremis	6.4	13.8	64.0	8.6	9.2	14.0	66.2	11.4	6.9	7.0	69.3	6.8	2.1	1.4	42.9	1.0
Acartia sp.	1.0	1.5	22.0	0.4	0.9	1.0	18.2	0.2	0.6	0.4	11.0	0.1				
Calanus marshallae	<0.1	0.9	2.0	<0.1	0.3	3.5	10.3	0.3	0.9	7.2	27.6	1.6	3.2	18.3	57.1	8.4
Calanus sp.					0.1	2.5	5.0	0.1	0.4	4.6	11.8	0.4	0.7	5.7	14.3	0.6
Centropages abdominalis	0.2	1.3	6.0	<0.1	0.2	0.9	8.9	0.1	0.3	0.8	14.2	0.1				
Eucalanus bungii					0.2	6.5	5.0	0.2	0.6	11.3	15.0	1.2	0.9	12.3	14.3	1.3
Metridia sp.	<0.1	0.9	2.0	<0.1	<0.1	0.4	1.3	<0.1								
Unident. copepodids <1.5 mm	14.4	20.3	96.0	22.1	15.5	15.3	95.7	21.8	17.6	11.6	95.3	19.8	19.4	8.6	85.7	16.3
Unident. copepodids >1.5 mm	<0.1	0.6	2.0	<0.1	0.4	2.9	12.3	0.3	0.8	4.3	24.4	0.9	1.6	6.1	42.9	2.2
Oithona sp.	18.5	10.2	76.0	14.5	12.9	4.9	80.8	10.7	7.6	1.9	76.4	5.2	9.2	1.6	100.0	7.4
Oncaea sp.	1.0	0.4	18.0	0.1	0.3	0.1	7.3	<0.1	0.1	<0.1	2.4	<0.1				

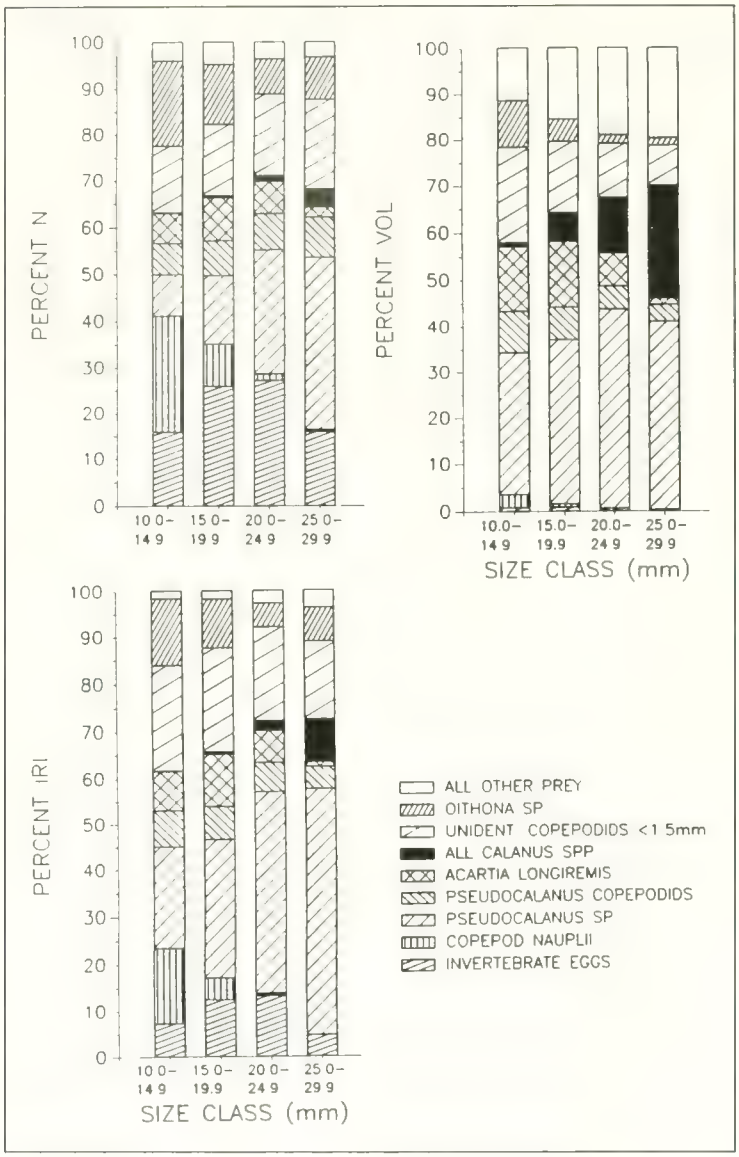

Figure 2
The diet of larval pollock in the Gulf of Alaska in June 1987, by size class, in terms of %*N*, %*VOL*, and %*IRI*.

Diet as a function of size

Small unidentified calanoid copepodids (i.e., <1.5 mm) were the primary prey (*IRI*) for larvae 10.0–14.9 mm SL, followed by *Pseudocalanus* sp. (Table 2, Fig. 2). Copepod nauplii, which ranked as a major food item for only this size class, was third in importance, followed by *Oithona* sp. and *Acartia longiremis*.

For larvae 15.0–19.9 mm SL, the same two prey items dominated the diet, but *Pseudocalanus* sp. was the most important item and small (unidentified) calanoid copepodids were second (Table 2, Fig. 2). Invertebrate eggs, *A. longiremis*, and *Oithona* sp. ranked third through fifth.

For fish 20.0–24.9 mm SL, *Pseudocalanus* sp. contributed twofold more to the diet than any other item (Table 2, Fig. 2). Small calanoid copepodids, invertebrate eggs, and *A. longiremis* were second, third, and fourth most important prey, followed by *Pseudocalanus* copepodids.

Pseudocalanus sp. continued to be the dominant prey for the largest size class that was examined, 25.0–29.9 mm SL, comprising over 52% of the diet, with small calanoid copepodids ranking second in importance (Table 2, Fig. 2). These were followed by *Calanus marshallae*, a species whose only major contribution to the diet was in this size class, *Oithona* sp., and *Pseudocalanus* copepodids.

Considering adult and copepodid forms together, *Pseudocalanus* sp. was the principal prey for all sizes of larvae and early juveniles (Table 2, Fig. 2). The contribution of *Pseudocalanus* sp. adults and all *Calanus* spp. increased directly in relation to fish size. On the

Table 3
Diet of larval walleye pollock in the Gulf of Alaska in 1987, by station, expressed as %*IRI*.

	Station number									
	21	30	32	38	40	42	44	45	48	58
Invertebrate eggs	6.5	0.3	16.7	12.4	1.4	28.3	13.3	26.1	6.9	0.2
Copepod nauplii	9.9	5.5	9.1	0.6	0.6	1.2	1.3	0.6	0.7	10.2
Barnacle nauplii		<0.1	0.1			<0.1	0.1			<0.1
Euphausiids	5.2	0.4	0.7	1.2	0.5	0.2	0.7	<0.1	<0.1	<0.1
Pteropods			10.7		0.9	<0.1	<0.1	<0.1		
Other	<0.1		0.4	<0.1	<0.1		<0.1			<0.1
Pseudocalanus sp.	23.3	4.5	7.4	32.8	5.2	31.4	39.2	50.0	49.1	41.2
Pseudocalanus copepodids	11.3	0.1	2.8	13.2	0.3	5.3	11.1	7.1	4.6	6.0
Acartia longiremis	1.7	22.2	7.9	5.6	53.7	4.5	5.8	1.0	6.1	11.2
Acartia sp.	0.1	0.2	5.1	<0.1		3.6	<0.1			<0.1
Calanus marshallae		0.5		7.0	0.2	<0.1	0.7	0.1	0.4	0.5
Calanus sp.	<0.1		0.1		<0.1			0.2	6.6	
Centropages abdominalis	<0.1	0.1	0.3	<0.1	0.1	0.2	<0.1		0.4	<0.1
Eucalanus bungii				3.1	13.5					
Metridia sp.	<0.1	<0.1					<0.1	<0.1		
Unident. copepodids <1.5 mm	16.1	37.8	15.7	16.7	17.2	22.7	23.3	13.2	21.7	20.1
Unident. copepodids >1.5 mm	<0.1	21.1		0.8	0.7	<0.1	<0.1	<0.1	0.4	0.1
Oithona sp.	25.7	7.2	22.7	6.5	5.6	2.4	4.4	1.6	3.1	10.4
Oncaea sp.	0.1		0.3	<0.1		0.1	<0.1	<0.1		<0.1

other hand, the contribution of *Pseudocalanus* copepodids and copepod nauplii decreased with increasing fish size. Other major prey categories (i.e., small calanoid copepodids, invertebrate eggs, *A. longiremis*, and *Oithona* sp.) showed no clear relation to fish size.

Diet as related to site of collection

Pseudocalanus sp. was the most important prey at 6 of the 10 stations, accounting for over 30% (*IRI*) of the diet at each of these locations (Table 3, Fig. 3). Small calanoid copepodids were of secondary importance, ranging from 13.2 to 23.3%, while invertebrate eggs, copepod nauplii, *Pseudocalanus* copepodids, and *A. longiremis* and *Oithona* sp. each contributed more than 10% to the diet at one or more of these stations.

At two of the remaining four stations *Oithona* sp. was the primary prey (22.7–25.7%). Small calanoid copepodids were most important at another staion (37.8%), and *A. longiremis* was dominant at the remaining one, comprising more than 53% of the diet. Additionally, invertebrate (mostly copepod) eggs, copepod nauplii, pteropods, *Pseudocalanus* sp., *Pseudocalanus* copepodids, *A. longiremis*, *Eucalanus bungii*, and small and large unidentified calanoid copepodids (i.e., >1.5 mm), were well represented in the diet at one or more of the stations that were not dominated by *Pseudocalanus* sp.

Diet overlap between stations

Values of the index of proportional similarity (*PS*) varied widely, franging from 0.252 to 0.833 (Table 4). Of 11 pairs of adjacent stations, 45% showed no significant diet overlap, while of 34 pairs of non-adjacent stations 50% showed no significant overlap. Two stations, 30 and 40, were quite dissimilar from all other stations, and station 32 showed significant overlap only in relation to stations 21 and 58.

When examining diet overlap for the six stations that comprise the transect parallel to the Alaska Peninsula, a high degree of variation was seen in *PS* values (Table 5). At the southwestern end of the transect the lowest *PS* value was obtained for stations in closest proximity (21 and 30), while at the northeastern end of the transect the greatest *PS* value was obtained for stations in closest proximity (58 and 44). At the same time, diet at the two most distanct stations (21 and 58) showed great similarity.

Along one of the two transects perpendicular to the Alaska Peninsula (stations 44, 45, and 48), *PS* values indicated considerable overlap (Table 6). In contrast, a different pattern was obtained along the other perpendicular transect (stations 38, 40, and 42) where *PS* values were wide-ranging. For each of the two transects the greatest diet overlap was between the nearshore and offshore extremes of the transect (i.e., stations 44 and 48, and stations 38 and 42).

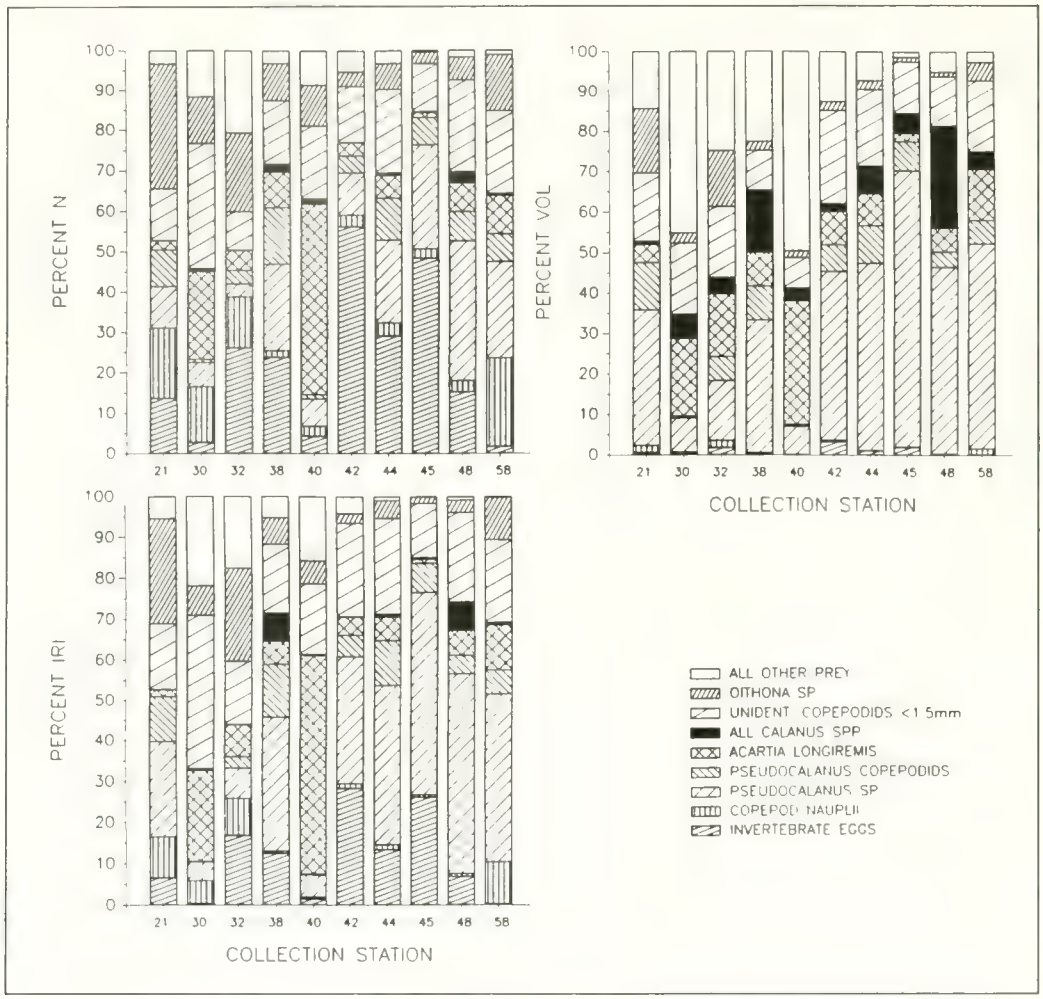

Figure 3
The diet of larval pollock in the Gulf of Alaska in June 1987, by collection station in terms of $\%N$, $\%VOL$, and $\%IRI$.

Table 4
Index of proportional similarity (PS) for walleye pollock 15.0–19.9 mm SL, at all stations, calculated using mean volume data. PS values for adjacent stations are underlined.

Sta. no.	21	30	32	38	40	42	44	45	48	58
21	*									
30	0.384	*								
32	0.605	0.504	*							
38	0.652	0.475	0.507	*						
40	0.303	0.577	0.433	0.519	*					
42	0.695	0.458	0.591	0.682	0.328	*				
44	0.770	0.474	0.524	0.742	0.353	0.833	*			
45	0.658	0.287	0.399	0.628	0.252	0.689	0.755	*		
48	0.676	0.415	0.490	0.676	0.368	0.760	0.805	0.728	*	
58	0.782	0.547	0.626	0.810	0.441	0.754	0.831	0.645	0.706	*

Table 5
Index of proportional similarity (PS) for walleye pollock 15.0–19.9 mm SL, along transect parallel to the Alaska Peninsula, calculated using mean volume data. PS values for adjacent stations are underlined.

Sta. no.	21	30	32	42	44	58
21	*					
30	0.384	*				
32	0.605	0.504	*			
42	0.695	0.458	0.591	*		
44	0.770	0.474	0.524	0.833	*	
58	0.782	0.547	0.626	0.754	0.831	*

Table 6

Index of proportional similarity (*PS*) for walleye pollock, 15.0–19.9 mm SL, along two transects perpendicular to the Alaska Peninsula, calculated using mean volume data. *PS* values for adjacent stations are underlined.

Sta. no.	38	40	42
38	*		
40	0.519	*	
42	0.682	0.328	*
	44	45	48
44	*		
45	0.755	*	
48	0.805	0.728	*

Discussion

The portion of the present study dealing with the relationship between diet and fish size complements the study by Kendall et al. (1987) conducted in the Gulf of Alaska during May 1983. As the samples in 1983 were collected earlier in the year using different gear (a 505-μm mesh bongo net) than in 1987, the size range of larvae was substantially different in the two studies. However, a comparison of the diet of larvae 10.0–19.0 mm can be made between the two years. From this it was clear that copepod eggs and nauplii were of some consequence in the diet in both years. A between-year comparison of the relative importance of *Pseudocalanus* sp. adults and copepodids cannot be made because the 1983 dietary analysis considered adult and immature stages together as copepodids (CI–CVI). In both years *Pseudocalanus* sp. was the dominant copepod, followed by *Acartia* sp. and *Oithona* sp. As *Pseudocalanus* sp. carries its eggs (Corkett and McLaren 1978), the majority of copepod eggs in the diet were probably incidentally ingested attached to adult females. However, berried females were not observed in pollock stomachs. While the delicate structure of *Pseudocalanus* egg sacs may preclude larval fish from ingesting females with eggs intact (A.J. Paul, Univ Alaska, Seward, pers. commun., Nov. 1988), it is also possible that some of the eggs that were ingested could have been from other genera such as *Acartia* or *Calanus* that broadcast their eggs into the sea (C.B. Miller, Oregon State Univ., Corvallis, pers. commun., June 1989). The source of copepod eggs cannot be resolved without observing female copepods with eggs in the diet or identifying eggs to species. Neither condition was met in the present study.

The dietary importance of copepod nauplii decreased and *Pseudocalanus minutus* increased with increasing larval size for larvae 9–20 mm SL in Uchiura Bay, Hokkaido (Kamba 1977), as was the case in the present study. However, while *A. longiremis*, *Oithona* sp., and various copepodids were important in the Gulf of Alaska, they were not in Uchiura Bay. Since copepod eggs were excluded from the dietary analyses by Kamba, it is not possible to compare their relative importance in Uchiura Bay with the Gulf of Alaska. In the Bering Sea, Clarke (1978) reported that copepod nauplii and *Oithona similis* were the primary prey for pollock 9–18 mm SL, and Cooney et al. (1980) reported that copepodids (CI–CVI) and copepod nauplii were dominant. *Oithona similis* was the dominant copepod species, followed by *Pseudocalanus* sp. and *A. longiremis*. In both Bering Sea accounts, copepod eggs accounted for approximately 5% of the diet of this size class, less than in the Gulf of Alaska.

While the diet of 20.0–29.9 mm SL fish in the Gulf of Alaska appeared to be more diverse than in Uchiura Bay (Kamba 1977), in both areas *Pseudocalanus* sp. was the dominant prey, and *Calanus* sp. was well represented in the diet. In the Bering Sea *Pseudocalanus* sp. copepodids were the dominant prey and copepod eggs were also very important in the diet of early juveniles, although a broader size class, 20.1–60.0 mm SL, was utilized (Cooney et al. 1980). In a more recent study, also in the Bering Sea, cyclopoid copepods proved to be the primary prey for fish 20.0–29.9 mm TL, with *Pseudocalanus* sp. adults second in importance (Lee 1985). In the Gulf of Alaska, *Oithona* sp. (the dominant cyclopoid) was of highly localized importance.

The manner in which diet of larval and juvenile pollock varied between different locales and between years in the same locale illustrates how diet may vary in response to available food resources, which vary in response to oceanographic conditions (e.g., Grover and Olla 1987). As plankton data for the present study were unavailable, the extent to which diet resulted from prey selectivity cannot be determined. However, assuming that diet was at least reflective of available food resources, the wide range in *PS* values would indicate that food resources were not homogeneous. Diet varied widely from station to station, with nearly as many nonadjacent as adjacent station pairs showing significant dietary overlap. This type of variation would suggest areas of planktonic patchiness, perhaps reflecting underlying hydrographic heterogeneities. Low *PS* values may indicate small prey patches, while high values that were seen across several stations may be indicative of large prey patches.

Regardless of whether prey were energetically equivalent at each station, the incidence of feeding was

100%. It is unclear whether differential growth rates may have resulted from the ingestion of different prey since growth rates were not measured in the present study. However, it remains a possibility since Yoklavich and Bailey (1989) reported differential growth rates for late larval and early juveniles at three locations in the Gulf of Alaska in 1987. These fish, which ranged from 12.8 to 40.8 mm SL, were collected in the same survey of late-stage larval pollock (Hinckley et al. 1989) as the present study, from 18 June to 15 July 1987. While specific collection stations differed between the two studies, Yoklavich and Bailey found that growth rates increased from southwest to northeast along the Alaskan Peninsula.

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Abstract.—Egg size has been shown to relate to survival and growth in the early life stages of fish. Combined field and laboratory studies examined variation in the egg size of walleye pollock *Theragra chalcogramma*, a commercially important North Pacific gadoid; and a preliminary assessment of the effect of egg size on larval size was made. Differences in egg size were found over parts of the geographical range, among years, and over the spawning season in Shelikof Strait. Egg size did not appear to correlate with female length, age, or condition. Individual female's egg size decreased significantly over the course of the spawning cycle. Preliminary studies in the laboratory showed that egg size is correlated with larval size and may therefore affect mortality in the early larval stages.

Variation of Egg Size of Walleye Pollock *Theragra chalcogramma* with a Preliminary Examination of the Effect of Egg Size on Larval Size*

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Variability in egg size may be an important factor in the survival of early life stages of fish. It has been proposed by numerous authors (Blaxter and Hempel 1963, Bagenal 1969, Ware 1975, Hunter 1981, Knutsen and Tilseth 1985) that egg size (dry weight or diameter) influences larval survival through its effects on larval size, growth rates, and activity. Larger eggs provide more energy for growth and development (Hempel and Blaxter 1967, Hempel 1979) and generally produce larger larvae which are able to avoid predators more effectively (Miller et al. 1988), survive longer without feeding (Hunter 1981), search a greater volume of water for prey (Blaxter 1986, Webb and Weihs 1986), and eat prey of a greater variety of sizes (Hunter 1981).

Differences in egg size are thought to reflect adaptations by the spawning stock to varying conditions met by early larvae. Bagenal (1971) proposed that there is a relationship among egg size, time of spawning, and availability of food. Cushing (1967) stated that egg size in Atlantic herring *Clupea harengus harengus* is related to the type of production cycle and its variability.

Hunter (1976) indicated that egg size may be important in studies of starvation and predation as cause of larval fish mortality, because of its effects on time to the onset of irreversible starvation, on feeding success, and on the ability of larvae to avoid predators. Larval size and its relation to egg size has been proposed as a unifying factor integrating the dynamics of larval survival and the mechanisms of recruitment. Miller et al. (1988), in their review of this subject, state that "...even small size differences of larvae at hatching can have significant ecological implications, and that even within a species (e.g., herring), size at hatching might be an adaptive response to local geographic conditions."

Walleye pollock *Theragra chalcogramma* is a semidemersal species ranging from Japan around the North Pacific rim to central California. This species supports important commercial fisheries in the Bering Sea and the Gulf of Alaska. Walleye pollock spawn pelagic eggs which have an incubation time of approximately 15 days in 5°C water. Egg diameters have been reported to range from 1.0 to 1.9 mm (Table 1). Larvae are 3–4 mm standard length (SL) at hatching (Dunn and Matarese 1987). Egg size in walleye pollock varies across its geographic range (Table 1). It also varies within populations (Gorbunova 1954, Yusa 1954, Nishiyama and Haryu 1981, Sakurai 1982), and over the course of the spawning season (Serobaba 1968). The causes and significance of egg size variation in walleye pollock are not well known.

This field and laboratory study assesses sources of variation in walleye pollock egg size and presents results of a preliminary study of the relation-

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Table 1
Geographic variation in walleye pollock egg size.

Location	Average latitude (°N)	Egg size (mm) Mean	Egg size (mm) Range	Temperature* (°C) (Mean)	Reference
Eastern Pacific					
Puget Sound	47	1.2	1.0–1.3	8.5	This study
Shelikof Strait	57	1.37	1.3–1.4	5.0	This study
Bering Sea	57	1.73	1.3–1.9	3.25	Nishiyama and Haryu 1981
Bering Sea	59	1.57	1.5–1.7	0.95	Serobaba 1968
Bering Sea	59	1.59	1.4–1.8	2.75	Serobaba 1974
Western Pacific					
Japan	38	1.45	1.2–1.7	8.0	Yusa 1954
Peter the Great Bay	43	1.46	1.3–1.7	2.0	Gorbunova 1954
S. Kurile Islands	45	1.53	1.3–1.8	1.43	Gorbunova 1954
N. Kurile Islands	48	1.61	1.4–1.8	1.17	Gorbunova 1954
Sakhalin Island	50	1.58	1.5–1.7	−0.08	Gorbunova 1954
W. Kamchatka	56	1.57	1.3–1.8	1.5	Gorbunova 1954

*Temperature at bottom or depth of highest egg abundance (averaged using minimum and maximum of reported range).

ship between egg size and larval size. Size variation in walleye pollock eggs due to annual, seasonal, and geographical factors was examined from eggs caught in ichthyoplankton surveys in the Gulf of Alaska from 1981 to 1986. Variation due to female age, length, and condition was studied using eggs taken from spawning females caught at sea and from females held in the laboratory. Effects of egg size on larval size at hatching and at yolksac absorption were investigated in rearing experiments, using eggs from captive females and eggs taken in ichthyoplankton surveys.

Methods

Field studies

Walleye pollock eggs were collected in the Gulf of Alaska between 1981 and 1986 with 60-cm bongo nets (0.505-mm mesh), deployed with standard MARMAP procedures (Posgay and Marak 1980).

Eggs selected for measurement were chosen from archived samples (Table 2) taken in different years (1981–86), months (March–May), and areas (Shelikof Strait, the Semidi Islands to the Shumagin Islands, and west of the Shumagin Islands; Fig. 1). Variation in mean egg size among individual sampling stations was examined by measuring 25–50 eggs from up to 10 stations per year/month/area combination. Eggs at similar stages of development (early blastula to early germ ring) were measured with an ocular micrometer on a dissecting microscope at 40× magnification. All eggs were preserved in 3–5% buffered formalin.

Because mean egg sizes were significantly different ($F = 4.75$, $p < 0.0005$) among sampling stations, nested analysis of variance models with unequal cell sizes were used to test year, month, and area effects, with stations as the nested factor. Variation in egg size among years (within area and month), among months (within year and area), and among areas (holding year and month constant) had to be tested separately, due to the incompleteness of the available dataset, including missing months and areas in some years (Table 2).

The General Linear Models procedure of SAS-PC (SAS Inst. 1985) was used in this analysis. The F-statistic was derived using the Satterthwaite approximation (Gaylor and Hopper 1969 as cited in Sokal and Rohlf 1981), except in one case where the criteria for using this test were not satisfied; in this case a simple approximation test (Sokal and Rohlf 1981) was used.

Effects of maternal age, size, and condition on egg diameter and dry weight were examined using eggs from females caught by midwater trawl in Shelikof Strait in late March, 1986 (Table 2). Hydrated (fully ripe) eggs were collected from spawning females, and preserved in 5% buffered formalin. For each female, fork length (FL), gonad- and liver-free body weight, and liver weight were determined and otoliths removed for ageing. Body weight and liver weight were used as indices of condition.

Sixty eggs per female were measured. Because hydrated eggs taken from the ovary are sometimes slightly nonspherical, egg diameters were measured on the axis that fell along the transect to make sure measurements were random. Five to ten eggs per fish were subsampled for dry weight; eggs were measured,

Table 2

Stratification of walleye pollock egg samples measured for differences in egg size by year, area, and month, and to examine the effect of female size, age, and condition on egg size. Samples were collected on ichthyoplankton cruises in the western Gulf of Alaska.

	Shelikof Strait			Semidi Is. to Shumagin Is.	West of Shumagin Is.
Year	March	April	May	April	April
1981	M	Y,M	M		
1982	M	Y,A,M	M	A	A
1984	M	Y,M	M		
1985		Y			
1986	F	Y			

Samples used to study the effect of year (Y), area (A), month (M), and female (F) age, size, and condition.

washed with distilled water, placed individually in preweighed aluminum boats, dried for 24 hours at 60°C, and weighed on a Cahn 29 electrobalance to the nearest 0.001 mg.

An analysis of variance procedure was used to examine egg size within and among fish. A multiple regression model was used to examine the effect of female length, age, and condition on egg diameter and egg weight. The factors in the regression were fork length, age, body weight (minus ovary weight and liver weight), and liver weight. The model used was

$$Y = B_0 + B_1X_1 + B_2X_2 + B_3X_3 + B_4X_4$$

where Y = egg diameter (mm) or egg dry weight (mg),
X_1 = fork length (cm),
X_2 = age (yr),
X_3 = body weight (minus ovary and liver weight, g),
X_4 = liver weight (g).

Interaction terms were not included in the model until after a test of the overall significance.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

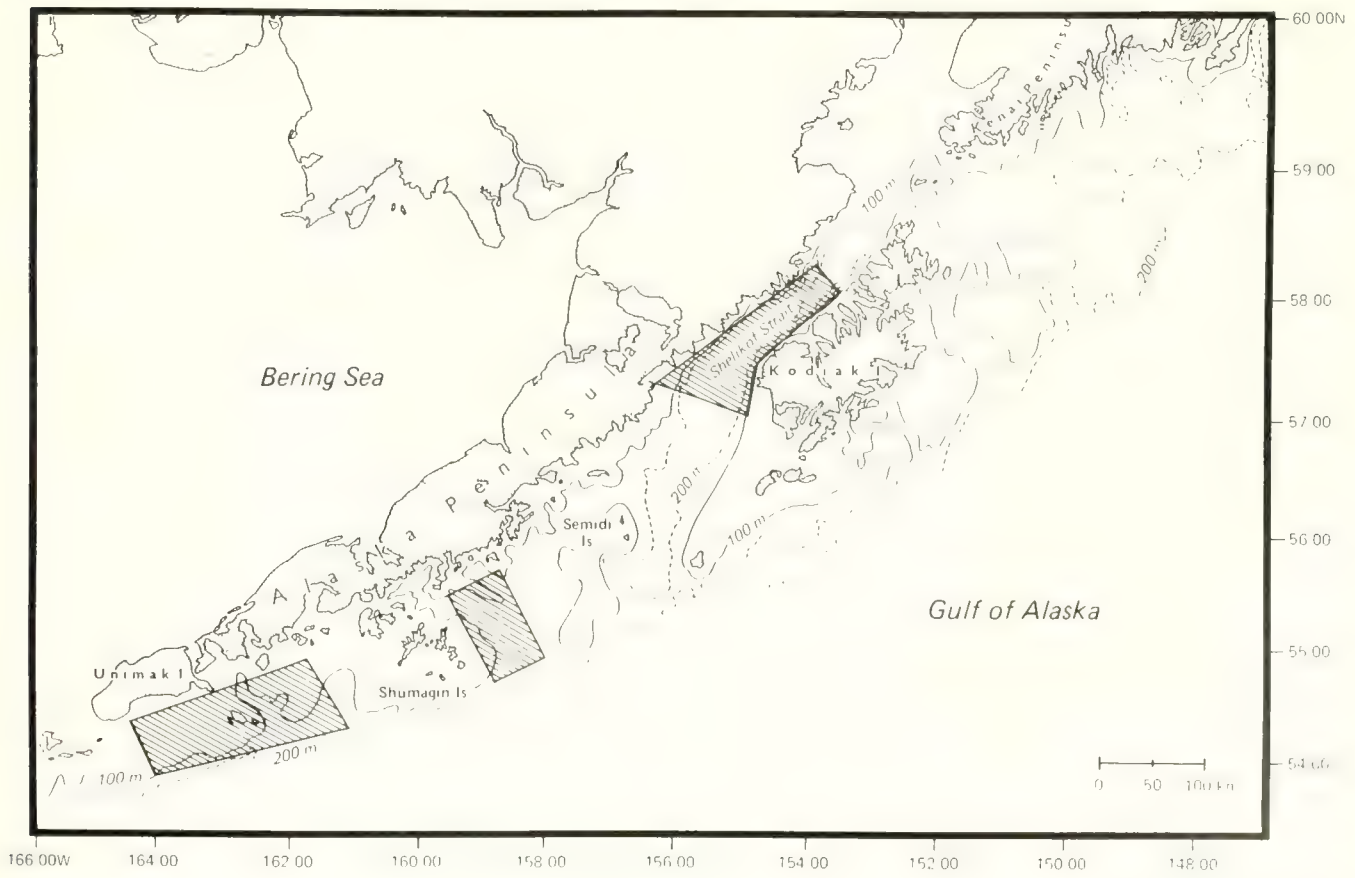

Figure 1

Western Gulf of Alaska, including Shelikof Strait, a major spawning area for walleye pollock. Shaded areas indicate regions from which samples were taken.

Laboratory experiments

Laboratory investigations were conducted using captive walleye pollock in March and April 1987. Adult prespawning walleye pollock were caught in January and February by handline in the Tacoma Narrows region of Puget Sound. Fish were transported to the laboratory and held in net pens under ambient light and temperature conditions and fed chopped herring *ad libidum* until they were nearly in spawning condition (i.e., eggs and milt were expelled with slight pressure to the abdomen). These fish were then transferred to individual 1700- or 2500-L tanks. One female and one or two males were placed in each tank and held throughout their spawning cycle. Water temperatures in the tanks were ambient and varied over the spawning season from 9.5 to 11.5°C ($\bar{x}$ 10.08°C). Ambient water temperature increased significantly (R^2=20.9%) over the experimental period. Salinity was constant at 28 ppt. A 20-cm plankton net with a hard codend was suspended in each tank to catch a sample of eggs from each spawning event. Plankton nets were checked each morning for the presence of eggs. If eggs were present in the codend, they were saved, and the water in the tanks replaced.

In 1988, pollock caught in Puget Sound were held individually in tanks to further examine the effect of female length on egg size. Eggs from the first batch from each of seven females were collected and measured in the same manner as described for the 1987 studies.

Egg diameters were measured on 15–25 unpreserved eggs, and egg dry weights were determined for 5–10 eggs from each spawning event. The remainder of the eggs were incubated separately (by female and spawning event) in 4-L jars filled with filtered seawater. The jars were placed in a water bath with running seawater at ambient water temperatures. Light levels were ambient. Water in these jars was changed several times during incubation (which lasted 6–9 days) and dead eggs were removed daily.

Six to fifteen larvae were collected on the day of hatch, anaesthetized with MS222, and their standard lengths measured. The rest of the larvae were held in the 4-L jars until yolksac absorption (defined as the point when individual larvae had used up 90–100% of their yolksacs). Standard lengths were measured (on anaesthetized larvae) and dry weights determined for 5–10 larvae at this stage.

A sample of live eggs collected from the ichthyoplankton in Shelikof Strait was transported to Seattle in April of 1987. Diameters and dry weights were determined on a subsample of these eggs and the rest were incubated. Larvae were measured at hatching and at yolksac absorption in the same manner as described above.

Table 3

Differences in mean walleye pollock egg diameter among years in April in the Shelikof Strait region of the Gulf of Alaska.

	Egg diameter			
Year*	Mean	SE	*N*	SNK grouping**
1981	1.360	0.003	320	A
1986	1.317	0.004	250	B
1985	1.299	0.004	250	C
1984	1.298	0.003	250	C
1982	1.296	0.004	249	C

*Data not available from 1983.
**Student-Newman-Keuls multiple range test (SAS Institute 1985). A, B, C indicate significantly different groups.

Eggs collected from the Gulf of Alaska ichthyoplankton surveys for examination of yearly, seasonal, and regional differences in egg size were preserved in 3–5% formalin. No correction factor was used to correct for changes in egg size due to preservation, as all eggs used in these analyses were preserved in the same manner. The field samples taken from spawning adults and used to examine the relationship between egg size and fish size, age, and condition were also preserved in 3–5% formalin. These, however, were collected before spawning, and the diameters may not be directly comparable to sizes of spawned eggs collected from the ichthyoplankton, due to possible changes in egg size at fertilization and activation (Fleming and Ng 1987, Kjørsvik and Lonning 1983). Eggs from the laboratory were measured fresh and are therefore not directly comparable with eggs from the field studies. The comparison between sizes of Gulf of Alaska eggs and Puget Sound eggs was made only on the fresh samples collected in 1987 from both areas.

Results

Geographical, seasonal, and regional differences in egg size

Examination of 1319 walleye pollock eggs from April plankton samples (the month when most spawning occurs; Kim 1987) collected in Shelikof Strait demonstrated a significant difference in mean egg diameters among years (F = 19.862, p<0.0005). Mean egg diameter was largest (Table 3) in 1981 and smallest in 1982; there was a 4.7% difference in size between these years. Mean egg size was not statistically different in 1982, 1984, and 1985 (SNK test, Table 3). Mean egg size was intermediate in 1986.

Table 4
Differences in mean walleye pollock egg diameter over the spawning season in Shelikof Strait for 1981, 1982, and 1984.

Year	Month	Egg diameter Mean	SE	*N*	SNK grouping
1981	March	1.405	0.007	103	A
	April	1.360	0.003	320	B
	May	1.297	0.005	204	C
1982	March	*			
	April	1.296	0.004	249	A
	May	1.314	0.006	159	B
1984	March	1.383	0.002	792	A
	April	1.299	0.004	250	B
	May	*			

*Data not available from these months.

Table 5
Differences in mean walleye pollock egg diameter by area within the Gulf of Alaska, April 1982.

Area	Egg diameter Mean	SE	*N*	SNK grouping
Shelikof Strait	1.397	0.003	348	A
Semidi Is. to the Shumagin Is.	1.361	0.004	348	B
West of the Shumagin Is.	1.296	0.005	249	C

Table 6
Correlation coefficients (r) between walleye pollock egg diameter and egg dry weight, and female length, age, body weight, and liver weight.

	Length	Age	Body weight	Liver weight
Egg diameter	0.210	0.245	0.080	0.171
Egg dry weight	0.294	0.297	0.125	0.070

A significant difference in mean egg diameters was also observed over the course of the spawning season (March–May) in Shelikof Strait (Table 4) in 1981 (F = 23.389, $p<0.0005$), 1982 (F = 16.3387, $0.01<p<0.025$), and 1984 (F = 54.105, $p<0.0005$*). In 1981 and 1984 egg sizes decreased over the course of the spawning season by about 7% per month (Table 4, $0.02<p<0.05$). In 1982, mean egg diameter apparently increased from April to May by 1.4%.

Unpreserved walleye pollock eggs collected from the plankton in the Gulf of Alaska (in April 1987) were larger in diameter ($\bar{x}$ 1.36 mm, range 1.30–1.41) and dry weight ($\bar{x}$ 0.120 mg, range 0.097–0.139) than fresh eggs from Puget Sound (diameter $\bar{x}$ 1.19 mm, 1.03–1.27; dry weight $\bar{x}$ 0.077, 0.052–0.092), which were spawned naturally in laboratory tanks in April 1987. Mean egg diameters from various parts of the spawning range within the Gulf of Alaska were also compared from collections in April 1982 (Table 5). Egg sizes differed among all of the areas examined (F = 18.854, $p<0.0005$). Egg sizes showed a decrease of 7.2% from Shelikof Strait westward to Unimak Pass.

Relationship between egg size and female characteristics

The mean diameter of hydrated eggs taken from Shelikof Strait females in 1986 was 1.41 mm (range 1.29–1.57). The mean dry weight of these eggs was 0.119 mg (range 0.095–0.148). Variation in egg diameter and egg dry weight among fish was more significant ($p<0.001$) than variation within fish. Correlation coefficients between egg diameter or egg dry weight and female length, age, body weight, and liver weight are presented in Table 6.

The multiple regressions of egg diameter and dry weight against fish length, age, body weight, and liver weight were nonsignificant (R^2 = 0.361, $0.10<p<0.25$, and R^2 = 0.321, $p>0.25$, respectively). A stepwise regression eliminated all variables as nonsignificant ($p>0.05$). No interactions or nonlinear relationships among variables were found. Fourteen females (29.5–47.0 cm FL) were held in the laboratory to investigate the female length-egg size relationship. As in previous regression analyses, no relationship was seen between female length and egg diameter for these fish (Fig. 2, r = 0.006).

Spawning characteristics and the relationship of egg size to larval size

The number of egg batches spawned per female in the laboratory in 1987 ranged from 2 to 21 over 3–26 days (Table 7). Excluding the two females which died prematurely, the average number of batches was 14.4 (range 9–21), and the average duration of spawning was 21.4 days (range 18–26). The average interval between batches for all fish was 2.1 days (range 1–5). The relationship between egg diameter and egg dry weight was linear ($p<0.0005$, R^2 = 0.630).

*Satterthwaite approximation not used in this test as the criteria were not met. A simple approximation test (Sokal and Rohlf 1981) was used in this case.

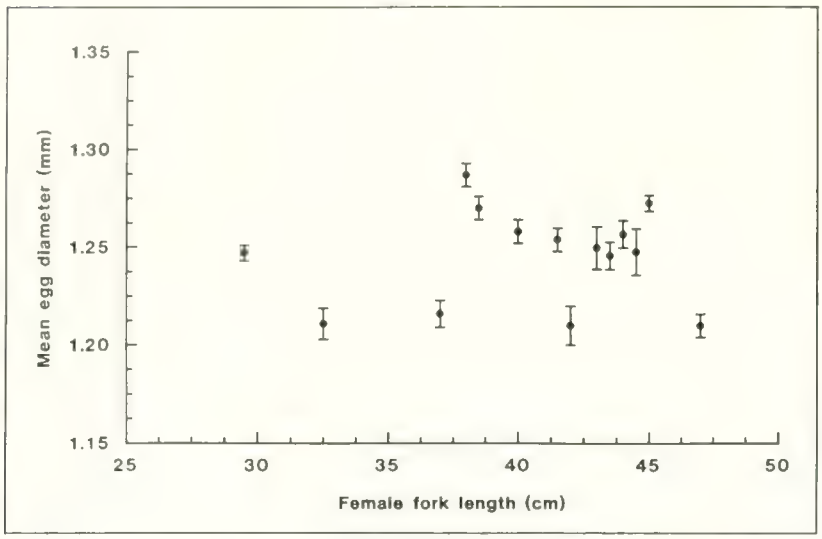

Figure 2
Relationship between female fork length and mean egg diameter in walleye pollock. Each dot represents the mean egg diameter from the first batch of eggs spawned from one female in the laboratory. Bars indicate standard error of the mean.

Table 7
Frequency and duration of spawning of captive walleye pollock from Puget Sound in 1987.

Female	Number of batches	Duration of spawning (d)	Interval (d) between batches: Mean	Interval (d) between batches: Range	Condition of ovary at death
1	9	20	2.2	1–5	>90% spent*
2	2	5	5.0		<10% spent**
3	13	18	1.4	1–2	spent*
4	15	23	1.5	1–3	spent*
5	2	3	3.0		<10% spent**
6	14	20	1.4	1–2	spent*
7	21	26	1.2	1–2	spent*
Mean	14.4***	21.4***	2.1		

*Sacrificed within 1 week of cessation of spawning.
**Died after 2 batches.
***Spent fish only.

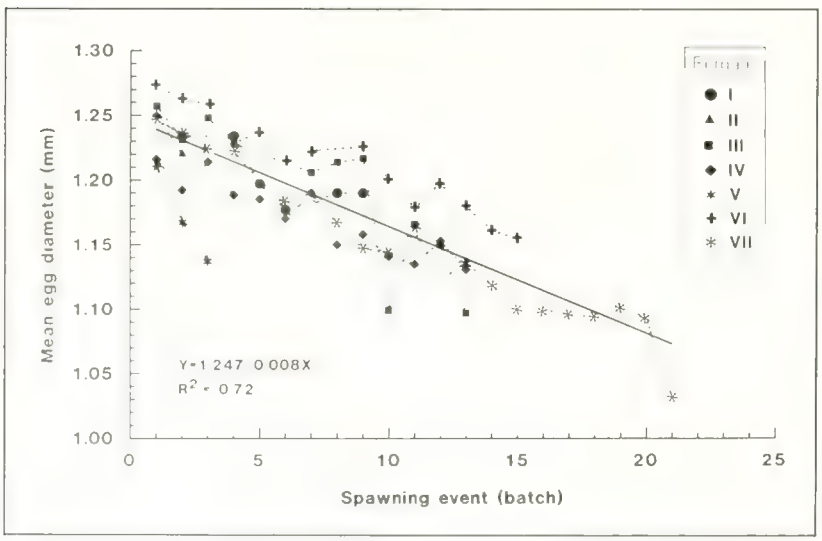

Figure 3
Change in mean egg diameter over the batch spawning cycle of female walleye pollock. Solid line indicates fitted regression line. Each symbol represents a separate female held in the laboratory over the spawning cycle.

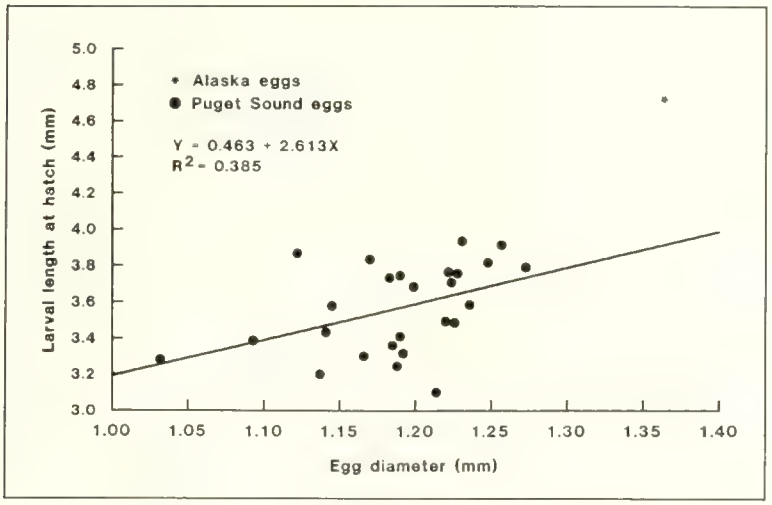

Figure 4A
Relationship between mean diameter of a batch of walleye pollock eggs spawned in the laboratory, and the mean standard length of larvae hatched from that batch.

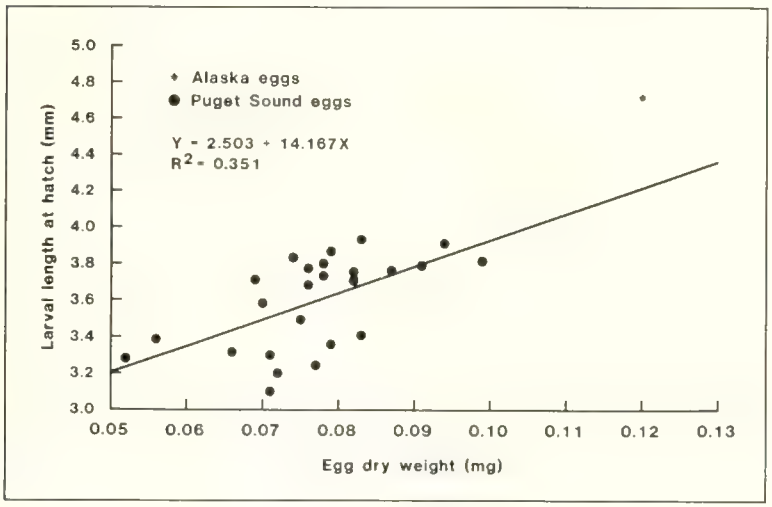

Figure 4B
Relationship between mean dry weight of a batch of walleye pollock eggs spawned in the laboratory, and the mean standard length of larvae hatched from that batch.

Mean egg diameter per batch of eggs spawned declined over the spawning cycle of an individual for all females (Fig. 3). The average decline in egg diameter over the batch spawning cycle (for females that completed spawning) was 0.14 mm, or 11.5% of the initial egg diameter.

Thirty-three batches of eggs were incubated and hatched. Larval standard length at hatch was positively correlated with egg diameter (Fig. 4A) and egg dry weight (Fig. 4B). The regressions of larval length at hatch on egg diameter and dry weight were both significant ($0.001<p<0.0025$, $R^2 = 0.385$, and $0.001<p<0.0025$, $R^2 = 0.351$, respectively).

Eighteen batches of larvae were raised to yolk-sac absorption and measured. The relationship between egg size and larval size at yolksac absorption was more variable than at hatch. Both egg diameter and dry weight were significantly correlated with larval length at yolksac absorption ($0.025<p<0.05$ and $0.005<p<0.01$, respectively; Fig. 5A, B).

Egg diameter varied positively with larval dry weight at yolksac absorption (Fig. 6A, $0.0025<p<0.005$, $R^2 = 0.462$), as did egg dry weight and larval dry weight at yolksac absorption (Fig. 6B, $p<0.0005$, $R^2 = 0.852$).

Discussion

Characteristics of spawning

The laboratory work from this study supports Sakurai's (1982) evidence that the batch spawning process in walleye pollock (which are partially synchronous spawners; Hinckley 1987) extends over a period of about a month, at least in the laboratory. Sakurai's walleye pollock, however, spawned approximately every 3 days, whereas walleye pollock in this study spawned about every 2 days. This probably reflects the effect of higher water temperatures in this study ($\bar{x}$ 10.1°C, versus 3.5–7.6°C in Sakurai's study). Higher temperatures have been shown to decrease the inter-

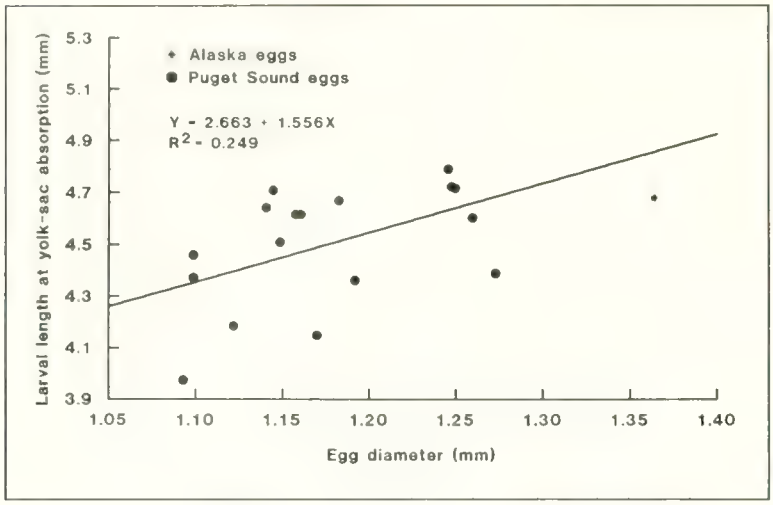

Figure 5A
Relationship between mean diameter of a batch of walleye pollock eggs spawned in the laboratory, and the mean standard length of larvae at yolksac absorption.

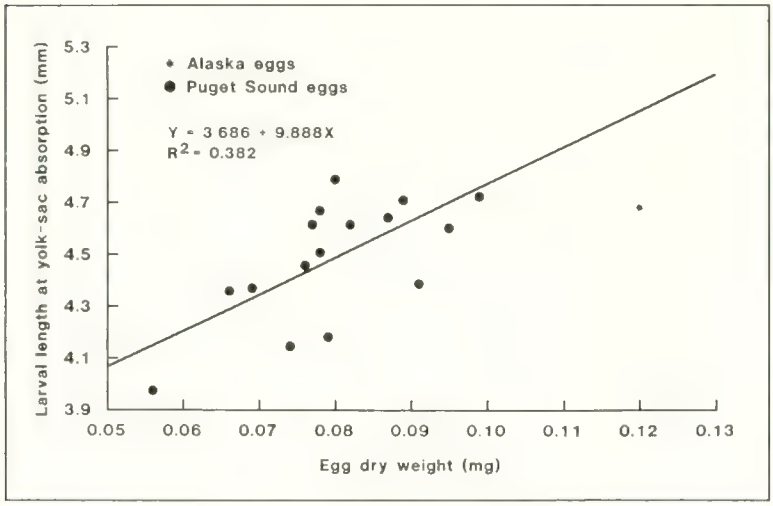

Figure 5B
Relationship between mean dry weight of a batch of walleye pollock eggs spawned in the laboratory, and the mean standard length of larvae at yolksac absorption.

val between batches of eggs spawned in Atlantic cod *Gadus morhua* (Kjesbu 1988).

Egg size variation within and among females

The laboratory studies showed that egg diameter in walleye pollock declined significantly over the spawning period of an individual. This was also shown by Sakurai (1982) for walleye pollock (over a limited portion of the spawning cycle) and for other gadoids by Hislop et al. 1978 and Moksness and Vestergård 1982 (*Melanogrammus aeglefinus*), by Grauman 1965 and Solemdal 1970 (*Gadus morhua*), and Hislop 1975 (*Merlangius merlangus*). The amount of decrease seen in walleye pollock, about 12%, was comparable with that seen in *Gadus morhua* by Kjesbu (1988) (7–15%) and with that in *Merlangius merlangus* by Hislop (1975) (9–14%). This decline may represent an adaptation by the parent stock to conditions faced by the larvae, as discussed later in this section.

Egg size in walleye pollock does not appear to be correlated with female length. The measurement of eggs from the first batch spawned (a method also used by Kjesbu (1988) for *Gadus morhua*) removes variation in egg size caused by the decline in egg size over the course of the spawning cycle, a problem which may have confused the results of other studies of the relationship between egg size and female size. Egg size in walleye pollock did not appear to correlate with female age or condition. Wet weights of body, gonad, and liver are not particularly sensitive indicators of condition in fish, however, and use of these measures may have obscured a correlation between these indices and egg size.

There are many contradictory studies on the egg size-female size relationship. Sakurai (1982, *Theragra chalcogramma*), Marsh (1984, *Etheostoma spectabilis*), Zilstra (1973, *Clupea harengus*), Solemdal (1970, *Gadus morhua*) and Ossthuizen and Daan (1974, *G. morhua*), and others did not find egg size-female size or age

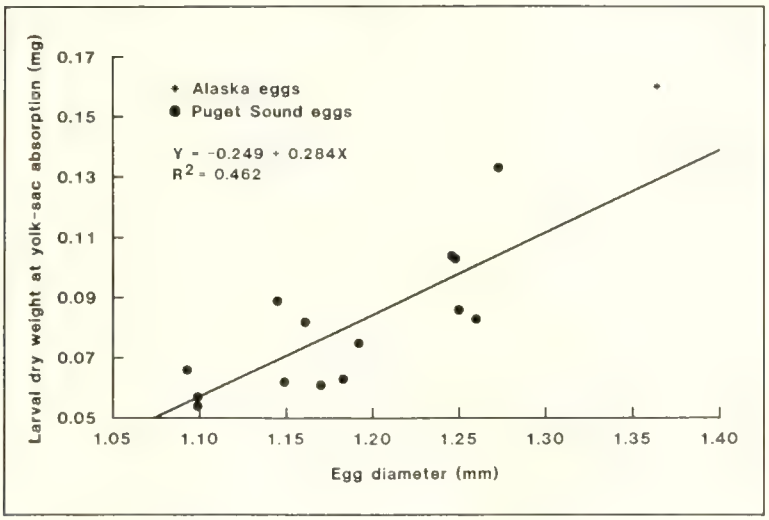

Figure 6A
Relationship between mean diameter of a batch of walleye pollock eggs spawned in the laboratory, and the mean dry weight of larvae at yolksac absorption.

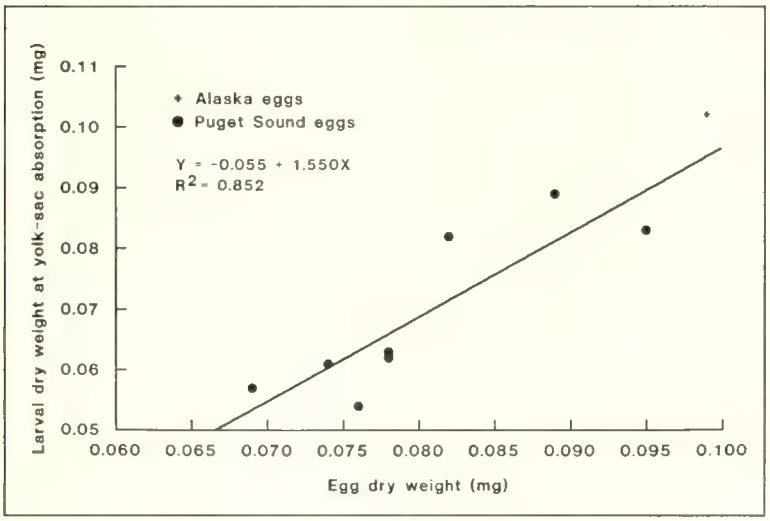

Figure 6B
Relationship between mean dry weight of a batch of walleye pollock eggs spawned in the laboratory, and the mean dry weight of larvae at yolksac absorption.

relationships in their studies. On the other hand, there are numerous studies in which egg size-female size relationships have been seen, such as Blaxter and Hempel (1963, *Clupea harengus*), Hislop et al. (1978, *Melanogrammus aeglefinus*), Grauman (1964, *Gadus morhua*), Kjesbu (1988, *G. morhua*), and many on salmonids. Some studies on the same species contradict one another with regards to this relationship. For those species showing a seasonal decline in egg size, an egg size-female size relationship may have been obscured in studies where this was not taken into account.

Within- and among-population variation in egg size

The population of walleye pollock spawning in Shelikof Strait shows significant seasonal and annual differences in egg size. The seasonal decline in egg size probably covaries with the decline over the spawning cycle. Annual differences in egg size during the peak spawning month (April) in Shelikof Strait appear to be significant. These yearly differences are apparently not attributable to changes in the size or age composition of the spawning stock, as no relationship between these factors and egg size is apparent.

It is possible that differences in the date of peak spawning in different years could change the mean egg size in the first week of April (when eggs measured for this study were collected). There is evidence that the mean date of peak spawning was later in 1986 and 1987 than in some earlier years (Yoklavich and Bailey 1990). The apparent difference in mean April egg size seen in this study could therefore be a reflection of the variability in time between peak spawning and egg collection and the decline in egg size over the spawning season, rather than a true interannual difference.

There appears to be a positive correlation between egg size and latitude in walleye pollock (Table 1). This correlation was also noted by Gorbunova (1954). In this study, this correlation was seen both among widely separated areas such as Puget Sound and the Gulf of Alaska, and within the Gulf of Alaska itself. Latitudinal clines in egg size have been seen by Demir (1963), Chiechomski (1973), and others, and have been discussed by Rass (1941), Marshall (1953), and Thresher (1988). As noted by Thresher, "Latitudinal variation in life histories of marine organisms typically are attributed to selection acting on local populations along a latitudinal environmental gradient..."

Several studies have noted an inverse relationship between egg size and temperature (Southward and Demir 1974, Ware 1977, Marsh 1984, Houghton et al. 1985, Imai and Tanaka 1987). Imai and Tanaka (1987), working with Japanese anchovy *Engraulis japonica*, found yearly changes in egg size which correlated with temperature, and were able, experimentally, to alter egg size during the spawning cycle of anchovy held in the laboratory by changing water temperature. Ware (1977) noted that peak spawning of *Scomber scombrus* occurs later if water temperatures warm more slowly than usual in the spring.

Temperature may be the latitudinal environmental gradient along which selection for egg size acts on local populations. The relationship between latitude and egg size appears to be correlated to temperature in the different spawning regions over the range of walleye pollock (Table 1). In the laboratory experiments on spawning done for this study, ambient water temperature increased over the spawning period, while egg size declined significantly for each female over this period. Mean monthly egg size and mean monthly water temperature at the depth where eggs are spawned (150 m to the bottom) within Shelikof Strait, however, show no apparent inverse correlation. There was also no inverse correlation between mean egg size in April and mean April water temperature at the depth of spawning over the years examined (J.D. Schumacher, Pacific Mar. Environ. Lab., Seattle, WA 98115-0070, unpubl. data). It may be that temperature acts on the parent stock at some earlier date, for example while the stock is migrating to the spawning grounds. Data are insufficient to investigate this question.

Consequences of egg size variation for larval survival

A correlation between egg size and larval size has also been noted in other species (*Clupea harengus*, Blaxter and Hempel 1963; *Salvelinus alpinus*, Wallace and Aasjord 1984; *Etheostoma spectabile*, Marsh 1986; *Gadus morhua*, Solemdal 1970, Knutsen and Tilseth 1985). Only a few studies have reported no correlation (Zonova 1973, Reagan and Conley 1977, Lagomarsino et al. 1988).

Egg size has been correlated with other larval factors. Growth rate, for example, has been seen to increase with increased egg size (Blaxter and Hempel 1963, Bagenal 1969, Wallace and Aasjord 1984, Moodie et al. 1989). This may be related to increased feeding success due to larger mouth sizes or increased search area (from increased reactive distance or swimming speed). Mouth size has been positively correlated with egg size (Blaxter and Hempel 1963, Shirota 1970, Knutsen and Tilseth 1985). Larvae with larger mouths are able to take larger or more varied sizes of prey items. Length of time from hatch to starvation (due to increased endogenous yolk reserves; Blaxter and Hempel 1963, Bagenal 1969, Theilacker 1981, Marsh 1986, Wallace and Aasjord 1984), and survival (Blaxter and Hempel 1963, Bagenal 1969, Pitman 1979, Small 1979, Moodie et al. 1989) have also been positively correlated with egg size. If larval survival is affected by larval size at hatch (Miller et al. 1988) and other factors, then variation in egg size in walleye pollock may cause differences in larval mortality rates.

It has been proposed that changes in egg size may be an adaptation to the timing of the production cycle, to ensure that larvae are produced that are able to take advantage of the available food supply (Cushing 1967; Hempel and Blaxter 1967; Bagenal 1971; Jones and Hall 1974; Ware 1975, 1977). The reproduction of zooplankton (such as copepods, e.g., *Pseudocalanus* and *Oithona* spp., whose naupliar stages constitute the most common food of first-feeding walleye pollock larvae in the Bering Sea and the Gulf of Alaska; Clarke 1978, 1984; Nishiyama and Hirano 1983; Kendall et al. 1987) is temperature and food related (Checkley 1980a, b; Durbin et al. 1983; Runge 1985; Corkett and McLaren 1978; Landry 1976). This implies that temperature would provide information on the timing of zooplankton reproduction, and therefore on the size of the available larval food supply (Ware 1977). Information on the changes in species and size composition of larval food sources in the western Gulf of Alaska is not presently available. The observed trends in egg size would be explained in terms of larval food supplies if the abundance of prey items increased and the size of food particles decreased and became more uniform as the season progressed.

The observed trends in egg size may also be a result of an adaptation to relieve predation pressure on eggs and larvae. Seasonal changes in egg size could result in changes in the predator-prey size ratio for eggs and larvae, affecting predation rates (Bailey and Houde 1989). This may not be important if egg predators are mainly planktivorous fishes. With zooplankton pred-

ators, however, small changes (10–20%) in egg diameter may affect their ability to handle or consume eggs. Also, if the abundance of egg predators increases, or they co-occur more frequently with eggs, then smaller but more numerous eggs (assuming a tradeoff between egg size and fecundity; Svardson 1949, Bagenal 1978) may be an adaptation to offset higher rates of predation later in the season.

Miller et al. (1988) have shown that predation rates are negatively correlated with larval size, possibly due to differences in predator mouth size, encounter rates of larvae and their predators, or the ability of larvae to escape predators. Trends in egg size and the resulting differences in larval size at hatch may, therefore, also be an adaptation to relieve predation on larvae, if the size, species composition, and co-occurrence of predators and larvae changes seasonally.

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Abstract.—Determining absolute survival rates for larval fishes is extremely difficult. However, many ecological questions concern relative survival of two groups. For example, we might ask: (1) Do older larvae have higher survival than younger larvae? and (2) Do faster growers have higher survival than slower growers? We present a simple model and several estimation schemes for the ratio of survival rates based on monitoring relative abundance of the two groups over time. When the logarithm of the ratio of abundances is regressed on time, the resulting estimate of slope is an estimate of the difference in instantaneous mortality rates. An estimate of the ratio of survival rates is obtained by exponentiating the slope. The model is shown to be a logistic model and can be fitted by maximum likelihood methods.

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Estimating Relative Survival Rate for Two Groups of Larval Fishes from Field Data: Do Older Larvae Survive Better Than Young?

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Determining absolute survival rates for larval fishes is extremely difficult, even when cohorts can be accurately identified by means of daily growth rings in the otoliths. For example, survival between times 1 and 2 might be estimated by catch/tow at time 2 ÷ catch/tow at time 1. Due to random sampling error alone, this estimate may be nonsensical (>1), and the chances of obtaining nonsensical estimates increases with increasing patchiness in the distribution of larvae over space.

In some cases, it may not be necessary to estimate absolute survival rates. Estimates of relative survival rate may be sufficient and easier to obtain. Many ecological questions concern the relative survival rates of two or more groups. For example, at a given point in time, the older larvae present should be larger than the younger larvae and, hence, may have a higher survival rate (Peterson and Wroblewski 1984, McGurk 1986). On the other hand, it has been suggested that larvae born later (i.e., younger larvae) may have a higher survival than larvae born earlier (Victor 1983, Methot 1983, Crecco and Savoy 1985, Rice et al. 1987). Also, it has been suggested that faster-growing larvae survive better than slower-growing ones (Rosenberg and Haugen 1982).

In this paper, we consider how relative survival rates can be estimated for two groups occurring at the same time and place from field data consisting of the composition of the catch at two or more times. The intuitive basis for the method is this: Changes in the relative abundance of two groups over time reflect differences in mortality rates (assuming no emigration or immigration occurs). The methods we present allow for catchability to differ for the two groups and to vary over time. However, the relative catchability (ratio of the catchability coefficients) of the groups cannot change over the time period considered. Thus, if factors such as wind, currents, boat speed, or net clogging vary among sampling periods, then the same proportional change in the catchability coefficient must occur for both groups. This is less restrictive than assuming constant catchability over time (as when estimating absolute survival rate by the decline in catch-per-unit-sampling-effort over time).

Development of the model

Suppose that at time t, a sample of larvae is obtained and that examination of the otoliths reveals that all larvae are of the same (approximate)

age. It is also determined that larvae can be classified as either fast or slow growing on the basis of the widths of the growth increments. Thus, we can determine the proportion of the larvae that are fast growing. If we sample the same population at time $t + 1$, we can again separate the larvae into fast- and slow-growing groups on the basis of the width of the otolith at time t (not at time $t + 1$).

Alternatively, suppose that a sample of larvae at time t has two cohorts, where a cohort is defined to be all larvae hatching in a given week. We can follow the relative abundance of the two cohorts in the catch over time by taking repeated samples from the population.

We will let the subscripts E and L refer to the two cohorts (e.g., E for early- and L for late-spawned). Let the number of larvae in the population's two cohorts at time t be N_{Et} and N_{Lt}. Suppose that the size of each cohort declines exponentially over time such that, for the ith cohort ($i \in \{E,L\}$),

$$N_{it} = N_{i0} \exp(-Z_i t)$$

where Z_i is the instantaneous mortality rate (time^{-1}) and N_{i0} is the initial abundance of the ith group. Also suppose that the expected catch of animals from group i at time t (C_{it}), for a standard unit of effort, is proportional to the abundance, i.e.,

$$C_{it} = q_{it} N_{it}$$

where q_{it} is the time- and group-specific catchability coefficient. Then the ratio of expected catches, R_t, is

$$R_t = \frac{C_{Lt}}{C_{Et}} = \frac{q_{Lt} N_{L0} \exp(-Z_L t)}{q_{Et} N_{E0} \exp(-Z_E t)}. \quad (1)$$

We assume that the ratio of the catchability coefficients (q_{Lt}/q_{Et}) is constant over the course of the study. Since the ratio of initial abundances (N_{L0}/N_{E0}) is also a constant, equation (1) can be rewritten

$$R_t = q \frac{\exp(-Z_L t)}{\exp(-Z_E t)} = q \exp\{(Z_E - Z_L)t\} \quad (2)$$

where q is a nuisance parameter that subsumes the catchability coefficients and initial abundances. Taking logarithms of (2) results in a linear relationship with respect to time:

$$\log_e(R_t) = \log_e(q) + (Z_E - Z_L)t. \quad (3)$$

Thus, regressing the logarithm of the observed ratio of abundances ($\hat{R}_t$) against time results in a linear relationship with slope equal to an estimate of the difference in the instantaneous mortality rates. (The proper weighting to use in a weighted regression is discussed below.) Note that it is sometimes necessary to add a small constant to the numerator and denominator to avoid dividing by 0 or taking the logarithm of 0.

Exponentiating the slope estimated by (3) provides an estimate of the ratio of the finite survival rates:

$$\widehat{S_L/S_E} = e^{slope}$$

where $S_L = e^{-Z_L}$; $S_E = e^{-Z_E}$.

By the Taylor's series (delta) method, the asymptotic variance of the estimated survival ratio can be approximated by (Seber 1982):

$$V(\widehat{S_L/S_E}) = e^{(2\ slope)}\ V(\text{slope}).$$

Diagnostics

Under the assumptions given above (constant ratio of catchabilities over time and constant difference in instantaneous mortality rates), a plot of the logarithm of the ratio of catches versus time would be expected to be linear (assuming the sample sizes are reasonably large). A departure from linearity suggests violation of one or both of the assumptions. This provides a diagnostic procedure to check on the assumptions. If catchabilities vary in a nonsystematic fashion, the fit of the regressions would be low and would not be influenced by increasing sample size.

Two-sample estimator

A special case is when only two samples have been obtained. Then, exponentiating the slope of the line described by equation (3) reduces to the change-in-ratio estimator of relative survival described by Paulik and Robson (1969). Thus,

$$\begin{pmatrix} \widehat{S_L} \\ S_E \end{pmatrix} = \frac{\hat{R}_2}{\hat{R}_1} = \frac{\hat{C}_{L2}\,\hat{C}_{E1}}{\hat{C}_{L1}\,\hat{C}_{E2}} \quad (4)$$

where the $\widehat{\ }$ symbol indicates estimated quantities. If the proportion of early spawners in samples 1 and 2 are denoted by P_1 and P_2, respectively, then an estimate of the variance can be found by the Taylor's series method to be (Seber 1982, p. 382)

$$V(\widehat{S_L/S_E}) = [P_1(1 - P_2)]^{-4} \{(1 - P_2)^2 P_2^2\, V(P_1) + (1 - P_1)^2 P_1^2\, V(P_2)\}.$$

Here, $V(P_1)$ and $V(P_2)$ are the variances of the proportions, found by the usual formula for variance of a binomial, i.e.,

$$V(P_i) = \frac{P_i(1-P_i)}{N_i}$$

where N_i is the number of larvae in sample i, and i can take on the values of 1 and 2.

Weighted regression

Equation (3) can be seen to be a logistic model by noting that $\log_e(R_t)$ is the logistic transformation. That is, letting P_t be the proportion in the sample at time t which belongs to group "L" (i.e., $\frac{C_L}{C_L + C_E}$), the logit transformation of the proportion is

$$\text{logit}(P_t) = \log_e\left(\frac{P_t}{1-P_t}\right) = \log_e(R_t).$$

This allows us to refer to known results for logistic models to determine the optimum weighting scheme.

Not all observations on catch composition are of equal value in estimating the relative survival rate. This is because the variance of the ratio of catches for any particular sampling date will be a function of the sample size and the proportions in the population. One method for specifying weights to be used in the regression, which explicitly accounts for this, is:

$$\text{weight}_t = \hat{C}_{Et}^{-1} + \hat{C}_{Lt}^{-1}.$$

When these weights are used in the regression, the resulting estimates are known as minimum logit chi-square estimates. Once the logistic regression model has been fitted, new weights can be computed using the predicted catch composition, rather than the observed composition. The regression can then be recomputed, the weights updated, and the regression recomputed. until adequate convergence is achieved. This procedure results in maximum likelihood estimates (McCullagh and Nelder 1983). Most standard statistical packages will perform logistic regression so that the user need not specify explicitly the iterative weighting scheme.

The above weighting scheme is appropriate when larvae are sampled randomly, i.e., each larva is sampled independently of all other larvae. This situation is approximated when the expected catch per tow is small (≤ 1) and tows are random over space. When the expected catches are large, the sampling procedure results in cluster samples. Consequently, the theoretical binomial variance is too small. However, the binomial variance becomes increasingly small as the sample size increases and as the proportions approach the extremes (0 or 1), and this is what would be expected for cluster sampling. Thus, weights computed from the binomial variance should be reasonably appropriate.

Estimation when there are many small samples

It sometimes occurs that catch rates are extremely low and many small samples are obtained. For example, sampling may be conducted daily with low intensity. In this case, the logistic regression procedure will not work well due to the occurrence of many zero catches. Estimation under the logistic model can still be accomplished by constructing the likelihood function and solving directly for the difference in mortality rates that maximizes the likelihood function.

The probability that an individual, randomly selected from the catch at time t, is from group E (early-spawning group) is equal to

$$\begin{aligned} P_t(E) &= \frac{\hat{C}_{Et}}{\hat{C}_{Et} + \hat{C}_{Lt}} \\ &= \frac{q_{Et} N_{E0} e^{-Z_E t}}{q_{Et} N_{E0} e^{-Z_E t} + q_{Lt} N_{L0} e^{-Z_L t}} \\ &= \frac{1}{1 + qe^{\Delta Z t}} \end{aligned} \quad (5)$$

where q is the "apparent" initial ratio of abundances (actual initial ratio of abundances if the ratio of catchability coefficients is equal to 1) and ΔZ is the difference in instantaneous mortality rates ($Z_E - Z_L$).

The probability that an animal is from group L is the complement of (5):

$$\begin{aligned} P_t(L) &= 1 - \frac{1}{1 + qe^{\Delta Z t}} \\ &= \frac{qe^{\Delta Z t}}{1 + qe^{\Delta Z t}}. \end{aligned}$$

The likelihood function can then be constructed as the product of the probabilities for each animal in each sample:

$$\begin{aligned} \Lambda &= \prod_{i=1}^{n_E} \frac{1}{1 + qe^{\Delta Z t}} \prod_{i=1}^{n_L} \frac{qe^{\Delta Z t}}{1 + qe^{\Delta Z t}} \\ &= \frac{q^{n_L} e^{(\Delta Z \sum_{i=1}^{n_L} t_i)}}{\prod_{i=1}^{n_E + n_L} (1 + qe^{\Delta Z t})} \end{aligned} \quad (6)$$

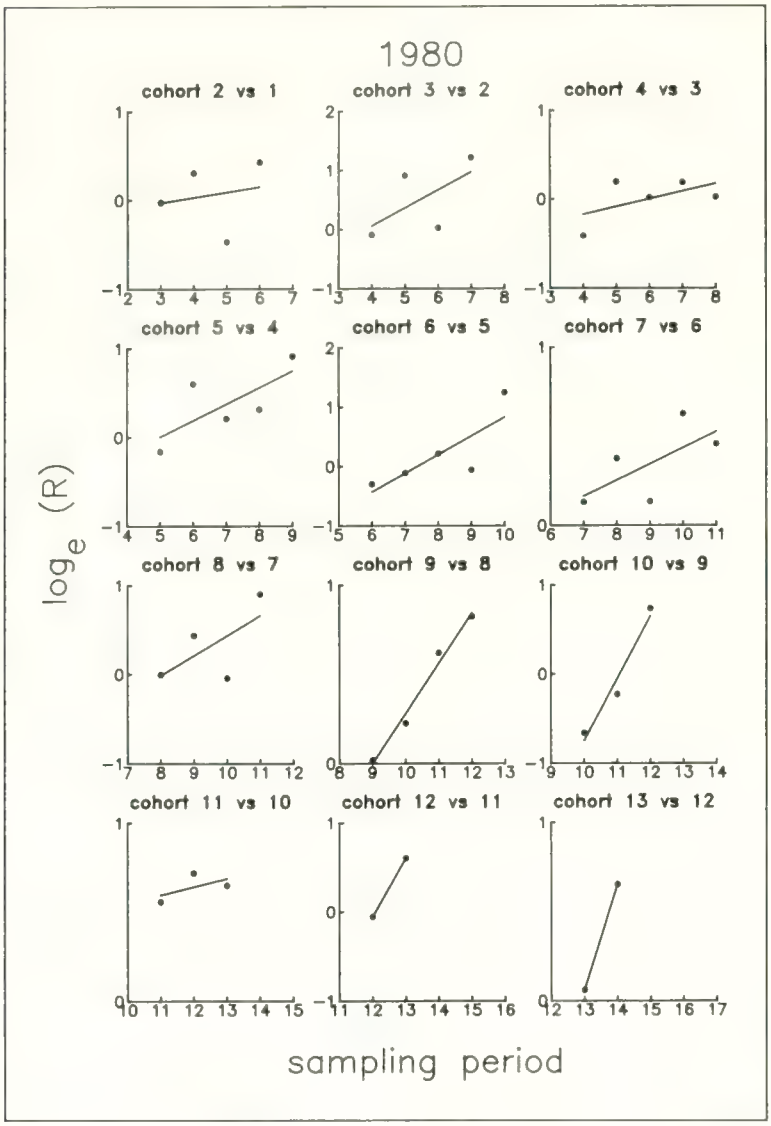

Figure 1

Plots of the logarithm of the ratio of abundance (cohort $i+1$ ÷ cohort i) versus sampling period (measured as 5-day intervals) in 1980. Slopes of the linear regression lines estimate $Z_E - Z_L$. (Note that the scale of the ordinate varies among plots.) In all 12 comparisons of cohorts, the slope is positive (later cohort has the better survival).

where n_E and n_L are the total number of animals observed in groups E and L, respectively, t_i is the time when the ith individual from group 1 was caught, and similarly for t_j. The major statistical packages have routines for maximizing this function.

Generalizations

The logistic model is easily extended to enable one to incorporate the effects of covariates. For example, suppose one has information on the time elapsed since the sampling program began (t) and also on the number of days (t^*) a power plant, which can be an additional source of mortality, has been operating for each of the sampling dates. Then instead of having t as the only explanatory variable, we can have a linear combination of explanatory variables in the exponent

$$\Delta Z t_i + b_1 t_i^*$$

where b_1 is the differential mortality rate (per time) of the two groups attributable to power plant operation.

Example

We consider data on American shad *Alosa sapidissima* in the Connecticut River, Connecticut, USA, kindly supplied by Victor Crecco and Thomas Savoy (Dep. Environ. Prot., Mar. Fish Office, Waterford, CT). A description of the study area and sampling methods, and a careful analysis of the data, are given in Crecco et al. (1983). Our purpose in considering these data is to illustrate the use of our method and to explore the kinds of questions that can be asked by study-

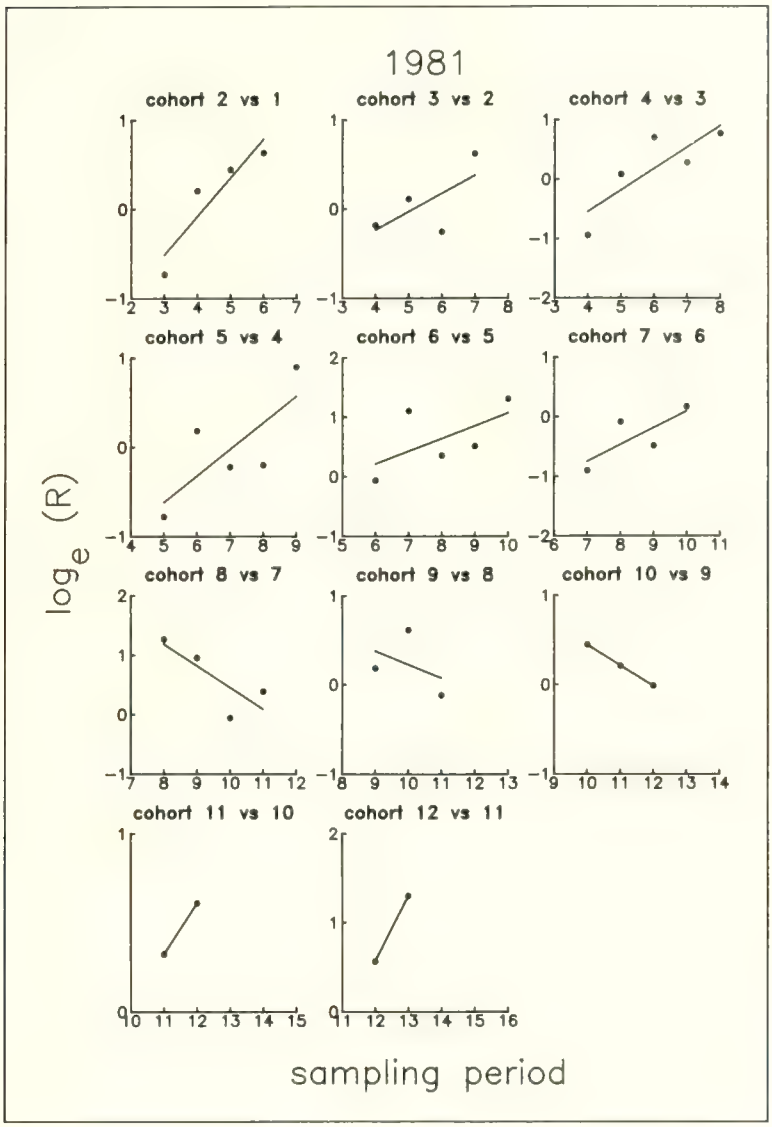

Figure 2

Plots of the logarithm of the ratio of abundance (cohort $i+1$ ÷ cohort i) versus sampling period (measured as 5-day intervals) in 1981. Slopes of the linear regression lines estimate $Z_E - Z_L$. (Note that the scale of the ordinate varies among plots.) In 8 of the 11 comparisons of cohorts, the slope is positive (later cohort has the better survival).

ing relative survival. For instance, Crecco and Savoy suggest that cohorts spawned later in the season have a higher relative survival based on comparison of larval and juvenile numbers. Our method provides a tool with which we can test this hypothesis for the larval stage while overcoming problems which may be associated with sampling variability or limited sample sizes.

Ichthyoplankton were sampled throughout the spring of 1980 and 1981. Approximately 30–40 larvae were aged for each 5-day sampling period. We compared the mortality of cohort $i+1$ with that of cohort i for all possible i where cohort i is defined to be animals born in the ith 5-day period of the season. This resulted in 12 comparisons for 1980 and 11 comparisons for 1981 (Figs. 1, 2). Because information on exact sizes of the samples was not available to us, we computed unweighted regressions. This provides unbiased estimates of the regression parameters, but the estimates are not of minimum variance and the standard errors are not accurate (Weisberg 1980).

The coefficients of determination were poor (r^2 range 4–98%, mean 55%, for comparisons with three or more observations) suggesting we cannot place much confidence in the magnitude of the estimates of differential mortality ($Z_E - Z_L$). This is undoubtably due to the very small sample sizes. However, it is worth noting that in 12 of the 12 comparisons using the 1980 data, the differential mortality was positive (see Figure 3), i.e., the survival rate of cohort $i+1$ (the later spawned cohort) was higher than the survival rate of cohort i (the earlier spawned cohort). Also, in 8 out of 11 comparisons using the 1981 data, the later-spawned cohort had the higher survival rate. If there were no differences in survival rates of the two cohorts in each

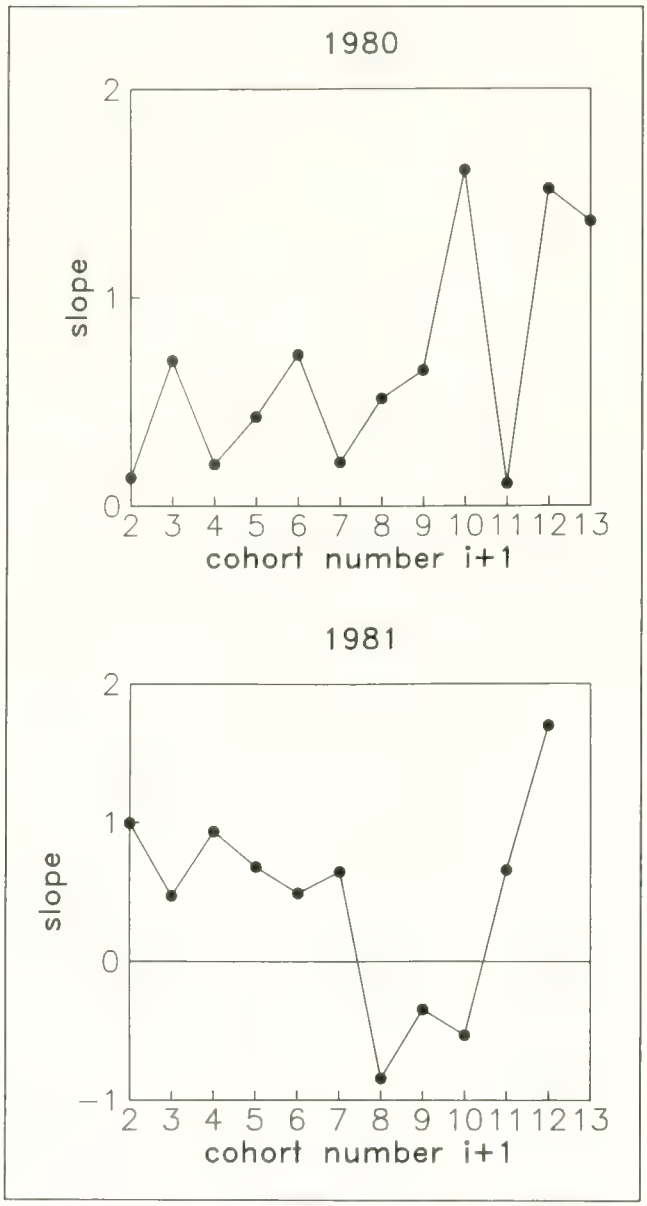

Figure 3

Plot of estimated differential mortality (i.e., Z for cohort $i+1$ minus Z for cohort i) versus cohort number, $i+1$. Differential mortalities are estimated as the slopes of the regressions in Figure 1 (top) and Figure 2 (bottom). Note that in all but three cases, the later-spawned cohort is estimated to have lower mortality (higher survival) than the earlier-spawned cohort.

pair, then one would expect half the comparisons would have a positive estimate of differential mortality and half would have negative estimates.

Discussion

We have presented three methods for estimating relative survival rates of larval fishes. The first method is based on a logistic regression model. It provides a graphic way to check the assumptions of constant relative survival and constant ratio of catchabilities. A special case of this method is the two-sample estimator of Paulik and Robson (1969) (our eq. 4). Explicit specification of the likelihood function (eq. 6) is necessary when many small samples are obtained, e.g., from a daily sampling program where the catch per tow is very small.

An intuitive method for estimating relative survival rate would be to estimate the absolute survival rate of each group by the decline in catch-per-unit-effort between two sampling times, and then to take the ratio of the two survival estimates. Thus,

$$\text{alternative estimate of } S_L/S_E = \frac{\hat{C}_{L2}}{\hat{C}_{L1}} \Big/ \frac{\hat{C}_{E2}}{\hat{C}_{E1}} = \frac{\hat{C}_{E1}\,\hat{C}_{L2}}{\hat{C}_{E2}\,\hat{C}_{L1}}. \quad (7)$$

The assumption necessary for the estimation of each survival rate is that the catchability has not changed over time. If one were to obtain an estimate of survival that is unfeasible (>1.0) one would be tempted to discard the data without computing relative survival. However, the expression to the extreme right in (7) is exactly equivalent to the two-sample estimator in (4). Thus, one can validly estimate relative survival rates even when estimates of absolute survival are obtained which are nonsensical. This is because the relative survival estimators do not require the catchabilities to remain constant over time, only the relative catchabilities.

On the basis of existing information, it is not possible to state quantitatively in what proportion of fish populations or in which situations late-spawning larvae will survive better than early-spawning larvae. In our example, sample sizes were quite small (~30–40 age determinations per 5-day sampling period) so that estimates of relative survival rate were imprecise. It is interesting to note, however, that in 12 of 12 comparisons in the 1980 data and in 8 of 11 comparisons in the 1981 data the later-spawned cohort (week $i+1$) had a higher survival rate than the earlier-spawned larvae (cohort from week i) (Fig. 3). However, our results indicate that late-hatching (smaller) larvae survive a given calendar period better than early-hatching (larger) larvae which is opposite to the general findings that larval fish mortality rates decrease with increasing size and/or age (Peterson and Wroblewski 1984, McGurk 1986). This suggests that whatever the cause of mortality (e.g., predation, transport), the vulnerability of larval shad in the Connecticut River to this factor increases with age and/or size during the period studied.

Our method was developed for the situation in which cohorts can be sampled simultaneously. Thus, if in a particular week gear efficiency was better than normal, any changes in catchabilities would tend to affect both cohorts so that the ratio of catchabilities might stay relatively constant. It may be tempting to use our method to compare cohorts over the same part of the ontogeny (i.e., cohorts of the same age occurring at different times of the season). However, in this situation there is no reason to believe that variations in catchability over time of the first cohort will be tracked by variations in catchability of the later cohort. Hence, there is no advantage in using our method over traditional methods of estimating absolute survival based on declines in catch-per-unit-effort.

Finally, we note that methods for estimating relative survival have wide applicability beyond the study of larval fishes. A classical problem is Lee's phenomenon in which back-calculated sizes at the first annulus do not agree with the observed sizes of the young fish. Jones (1958) proposed as explanation that faster-growing fish may have a different mortality rate than slower growers. This can be studied by observing the proportion at each age that have a small back-calculated size at the first annulus. Hoenig and Lawing (1983) describe how the logistic model might explain the occurrence of progressively skewed sex ratios with age. Differential survival has been studied by a variety of mark-recapture methods in the context of fitness and natural selection (see Manly 1985) and as a means of estimating impacts of power plants (see Burnham et al. 1987). Another application is to the evaluation of stocking success as related to genetic strain of fish or hatchery treatment. That is, the ratio of abundances of two strains can be monitored over time to study whether one strain survives better than the other.

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Abstract.—The horizontal and vertical movements of yellowfin tuna *Thunnus albacares* and bigeye tuna *T. obesus* captured near fish-aggregating devices (FADs) were determined using pressure-sensitive ultrasonic transmitters. The movements of these FAD-associated fish were compared with the tracks of yellowfin tuna not associated with FADs. Tracks from 11 yellowfin and 4 bigeye tuna were obtained; these included 23 complete 24-hour periods of observation. Whether associated with FADs or a 40-fathom (75-m) reef dropoff, most yellowfin and bigeye tunas exhibited similar diurnal patterns. The fish tended to remain tightly associated with FADs or the reef dropoff during the day, move away at night, and return the next morning. The maximum range of these nighttime excursions averaged approximately 5 nmi. These tunas apparently treated the FADs as outliers of the coastal topography. This may not be the same behavior that results in the association of these species with drifting objects such as logs. Tuna can learn FAD positions and navigate precisely between FADs that are at least 10 nmi apart. When not associated with FADs or the 40-fathom dropoff, yellowfin tuna oriented to the bottom of the mixed layer (50–90 m) in daytime, whereas the bigeye occupied depths between 190 and 250 m. The daytime distribution of bigeye tuna seemed to be influenced by the depth of the 15°C isotherm. Both species swam closer to the surface at night. Swimming strategies possibly associated with energy and thermoconservation were observed.

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Horizontal and Vertical Movements of Yellowfin and Bigeye Tuna Associated with Fish Aggregating Devices*

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Tropical and subtropical pelagic fishes aggregate around natural, drifting debris such as logs and mats of algae. Man-made, anchored floating objects, known as fish aggregating devices (FADs), have also proven effective in attracting and holding commercially important pelagic species (Shomura and Matsumoto 1982, Matsumoto et al. 1981, Brock 1985). Species commonly found around FADs in Hawaii are yellowfin tuna *Thunnus albacares*, bigeye tuna *T. obesus*, skipjack tuna *Katsuwonus pelamis*, dolphin or mahimahi *Coryphaena hippurus*, and wahoo or ono *Acanthocybium solandri*. The first commercial FADs were deployed in the calm waters of the Philippines in the early 1970s to attract yellowfin tuna (Kihara 1981), and in 1977 experimental FADs designed for use in high-energy, deep-water environments were anchored around the Hawaiian islands (Matsumoto et al. 1981). Due to the success of these bouys in aggregating fish, FADs have come to play an important role in the commercial, subsistence, and recreational fisheries of all the tropical and sub-tropical oceans of the world.

Despite the widespread use of FADs, left unanswered are important questions concerning their range of influence, optimal placement, and impact on surrounding fish populations. The behavioral patterns that result in fish being associated with floating objects of any type are poorly understood and not widely agreed upon (Gooding and Magnuson 1967, Hunter and Mitchell 1967, Fedoryako 1982). However, the underlying mechanisms of aggregation have generally been assumed to be the same for both free-floating phenomena such as logs, and anchored man-made objects such as FADs (Shomura and Matsumoto 1982). To better understand the behavior of tunas associated with FADs, the movements of yellowfin and bigeye tuna caught within 500 m of these devices were tracked using pressure-sensitive ultrasonic transmitters. The movements of these fish were compared with those of tunas that were not associated with FADs, but with the reef perimeter surrounding the islands. In Hawaii and elsewhere in the Pacific, yellowfin tuna can be found in the vicinity of the 40-fathom (75-m) isobath where the island topography abruptly descends into very deep water. In fact, the dropoff of the outer reef edge is often so steep that

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the horizontal distance between the 40-fathom and 100-fathom (187-m) isobaths is measured in tens of meters. To observe the behavior of non FAD-associated tuna, three yellowfin tuna were tracked that were caught on or near the 40-fathom isobath around Oahu, Hawaii.

The influence of FADs on the vertical movements of these species was investigated by comparing the depth distributions of the two species in on-FAD (within 500 m of a FAD) and off-FAD (beyond 500 m of a FAD) situations. The depth distributions were analyzed with respect to ambient ocean temperatures, as measured by expendable bathythermographs.

Methods

The horizontal and vertical movements of individual fish were monitored by pressure-sensitive, 50 KHz ultrasonic transmitters (Vemco, Halifax, Nova Scotia, Canada). Fish caught on the tracking vessel by trolling and pole-and-line techniques were fitted with transmitters by passing two nylon "tie-wraps" through the dorsal pterygiophores and trunk musculature adjacent to the second dorsal fin (Fig. 1). The fish were out of the water for approximately 1 minute during this procedure. The fish were then released and followed using a directional hydrophone mounted on the tracking boat. Whenever possible, a distance of approximately 200 m was maintained between the fish and the boat. Geographic position was determined every 15 minutes by a combination of Loran-C, radar, bathymetric, and visual fixes. These techniques evolved from pioneering work in tuna tracking by Yuen (1970), Laurs et al. (1977), Carey and Olson (1982), and Carey (1983). A summary of previous ultrasonic tracks of tuna has been compiled by Hunter et al. (1986). A detailed account of the methods used in the current study has been published previously (Holland et al. 1985, Bayliff and Holland 1986).

The transmitters were equipped with pressure sensors, which modulated the rate of pulse transmission in response to changes in water pressure (depth). Thus, vertical movements of the fish were determined by measuring the time between signal pulses. These pulses were recorded on audiocassettes for analysis ashore. Expendable bathythermographs deployed approximately every 3 hours provided ocean temperature profiles, which were superimposed on the vertical movement plots. Pooled time-at-depth and time-at-temperature histograms were constructed from all tracks combined, using 10-m and 1°C bins averaged every 10 minutes. The data were analyzed for daytime and nighttime depth distributions. Differences in the temperature and depth distributions for day-versus-night and on-FAD versus off-FAD were analysed by factorial analysis of variance (SAS General Linear Models Procedure, SAS 1985). Portions of tracks occurring on-FAD or near the reef dropoff were not included in these calculations. Thus, the depth histograms and overall averages are compiled from movements that were not constrained by bottom topography or influenced by the presence of floating objects.

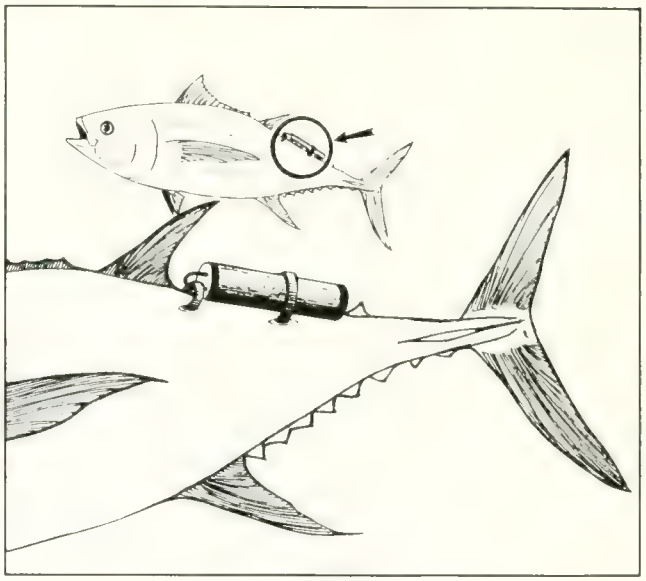

Figure 1
Transmitters were attached to yellowfin and bigeye tuna with two nylon straps inserted through the dorsal musculature and pterygiophores associated with the second dorsal fin (from Holland et al. 1985).

The tracking techniques used in this study are not capable of detecting small-scale changes in the horizontal swimming direction of the fish. Consequently, sustained swimming speeds have been calculated only from sections of tracks in which fish demonstrated prolonged straight-line movements. Swimming speeds were calculated as distance traveled per unit time and in terms of body lengths (fork length, FL) per second. Swimming speeds were calculated for each complete hour of "staight" running; these hourly rates were averaged to yield a sustained swimming speed for the relevant section of each track. Vertical movements were not included in these calculations.

Daytime and nighttime time-at-temperature histograms were generated for both yellowfin and bigeye tuna. Because of differences in absolute ocean-surface temperatures between different tracks, and because of

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previous indications that ocean thermoclines may be important orientation cues for tuna (Carey and Olson 1982), the time-at-temperature data were analyzed relative to the surface mixed layer. Thus, the mixed layer is referred to as ML, and the progressively colder 1°C isotherms as ML-1, ML-2, and so on.

Results

The results reported here are from tracks of 11 yellowfin and 4 bigeye tuna. Duration of tracks from release to track termination ranged from 5 hours to 6 days, with an average duration of 31.6 hours. Overall, these tracks encompass 23 complete 24 hour periods of observation. All 4 bigeye and 8 of the 11 yellowfin tuna were caught within 500 m of FADs. The remaining three yellowfin tuna tracks were from fish caught on or near the 40-fathom contour around the island of Oahu.

Horizontal movements

For yellowfin tuna, a clear pattern of horizontal movement was apparent. That is, during daylight the fish usually moved within a home range, staying in proximity to certain well-defined physical features, such as FADs or the outer reef dropoff. Eight of the 11 yellowfin tuna and 2 of the bigeye tuna showed aspects of this behavior, and this pattern was exhibited by both the FAD-associated and coastline-associated fish. Most of these fish made diurnal movements away from these daytime haunts, with the initial change in location often occurring around sunset.

FAD-associated yellowfin tuna These tuna spent daylight hours very close to the FADs, and then left those locations sometime between late afternoon and early nighttime to embark on extensive nighttime excursions, returning to the same or another FAD the following day. Five of the eight FAD-associated yellowfin tuna displayed aspects of this diurnal on-FAD and off-FAD behavior. A sixth FAD-associated fish showed signs of displaying this behavior, but was lost before this could be confirmed. The following is a brief synopsis of their horizontal movements.

Yellowfin tuna YF8404 (51 cm FL) was caught and tagged at V FAD at 0927, and stayed within 100 m of the FAD for 11.3 hours before leaving it a few minutes after sunset (1925, Fig. 2A). The fish then made a nighttime excursion totaling 12 nmi before returning to within 100 m of the FAD by 1312 the next day. During the last few hours of this approach the fish moved very slowly, as if it was drifting in the prevailing current. Once at the FAD, the fish again stayed close to the buoy until departing at sunset on a second

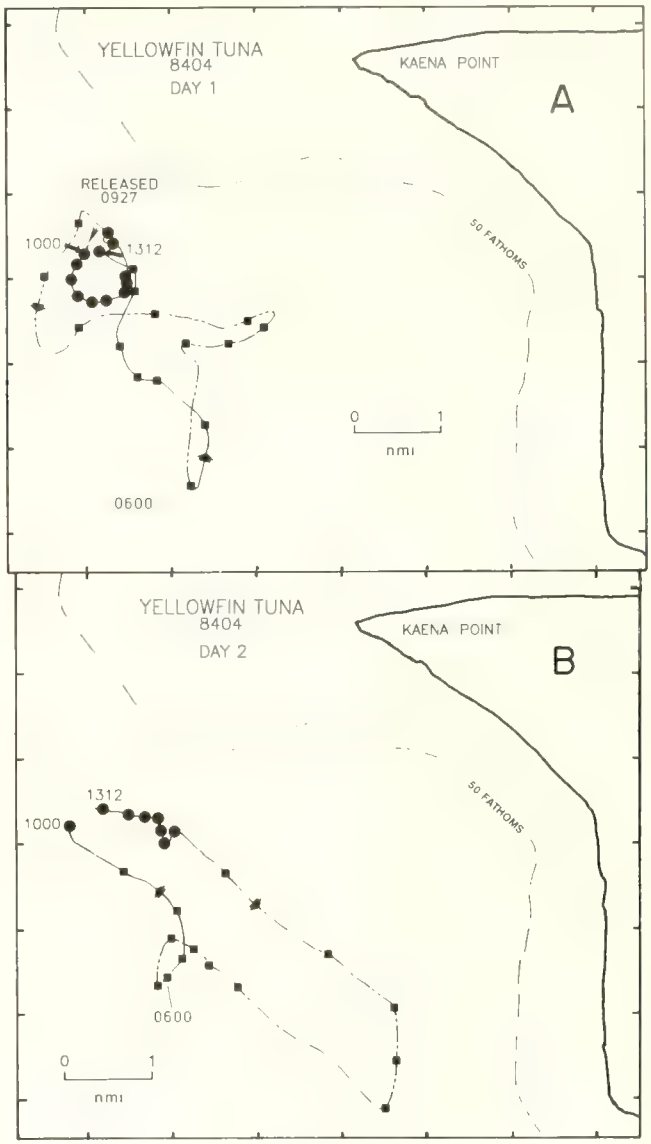

Figure 2

(A) 48-hour track of yellowfin tuna YF8404 tagged and released at 0927 at V FAD, Oahu. Circles = hourly marks when fish is on-FAD; squares = hourly marks when fish is off-FAD. In this and subsequent figures, solid line = daytime movements, dashed line = nighttime movements, and marks on figure axes = 1° divisions. On the first day (A) the fish remained very close to the FAD as it moved in a circular path in the current, departed the FAD after nightfall, and returned at 1312 the following day. The second day's behavior (B) was similar, despite a different pattern of movement by the FAD.

nighttime excursion of 11.25 nmi. The maximum distance away from the FAD was 3.0 nmi on the first night and 5.0 nmi on the second. On both excursions, the fish commenced moving back toward the FAD immediately after sunrise (Fig. 2A, B).

Two hours after fish YF8504 (47 cm FL) was tagged and released at S FAD at 0551, it made a 4-hour, 1-nmi excursion away from the buoy before taking up a posi-

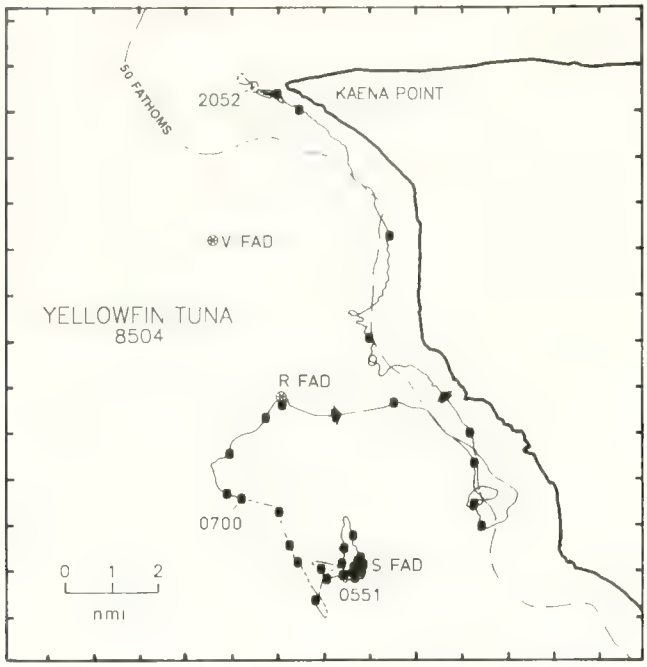

Figure 3

Yellowfin tuna YF8504 spent 8 daylight hours on the upcurrent side of S FAD before moving away at night. The next morning it moved to R FAD until disturbed by a school of porpoises, when it immediately took a direct course to the island dropoff, which it patroled for the rest of the day. In this and subsequent figures, squares = hourly position marks.

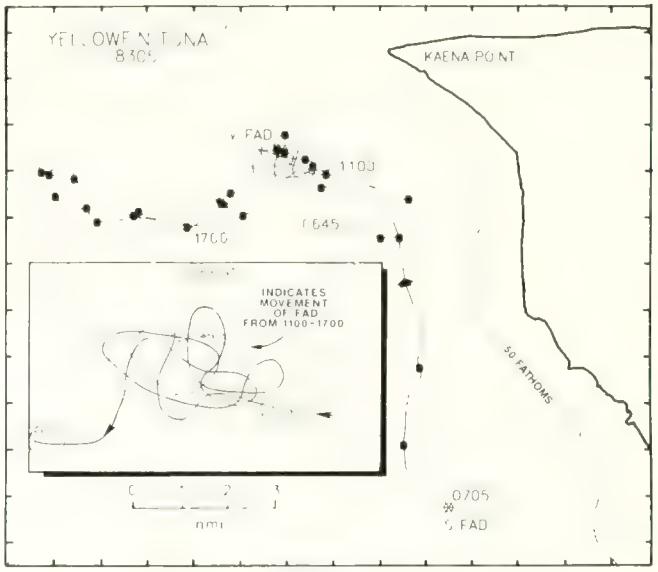

Figure 4

Yellowfin tuna YF8305 departed S FAD immediately after release at 0705 and took a direct course to the next nearest FAD, V (R was off station at the time), where it patroled almost exclusively in the upcurrent area (insert) before making an overnight excursion totaling 15 nmi.

tion within 50 m of the FAD for the remaining 8.0 hours of daylight (Fig. 3). During this time the fish was almost exclusively on the upcurrent side of the bouy. At 2345 the fish left the FAD and moved offshore; by sunrise the next day, it was 3.25 nmi from S FAD. The fish then moved 3.0 nmi in a direct course to the nearest adjacent FAD (R) arriving there at 0910. Once there, it stayed extremely close to the FAD and in the company of a school of other yellowfin tuna that could be seen from the surface. At 1020 a group of porpoises arrived and dove through the school of tuna, which appeared to scatter in all directions. The tagged fish dove and swam to the 40-fathom contour of the island, where it stayed for the rest of the day. Contact was lost just after sunset on the second night.

Fish YF8305 (55 cm FL), after being tagged and released at S FAD at 0705, swam for 4.0 hours on a direct course to V FAD, approximately 10 nmi away from the release point (Fig. 4). The fish spent 95% of the next 5.0 hours moving around on the upcurrent side of this FAD. In the late afternoon, the fish departed the FAD and spent most of the night farther offshore, moving in a 15-nmi loop before heading back toward V FAD the following morning. Just after first light, when the fish had returned to within 2 nmi of the FAD and appeared to be headed back even closer, the transmitter was shed.

The tracks of fish YF8406 (62.5 cm FL) and YF8501 (44.0 cm FL) were similar. During the daytime, both fish stayed very close to their respective FADs (for 9 and 12 hours, respectively), and both were lost at sunset in deteriorating sea conditions. Because there was no evidence of transmitter failure, and exhaustive searches at the FAD locations after dark failed to relocate the signal, it is reasonable to assume that both these fish were lost when they made sudden evening departures from the vicinity of their respective FADs.

Fish YF8302 (64 cm FL) was caught and tagged at S FAD, but lost 5.0 hours later. When contact was lost, the fish had departed the release site, but appeared to be curving back toward the bouy.

Fish YF8502 (74.5 cm FL) was similar to other FAD-associated yellowfin tuna in that, for the first 5.0 hours of the track (0600–1100), it stayed in close proximity (within 100 m) to S FAD. However, it then moved steadily away but was lost 12 nmi southwest of the buoy due to equipment failure after 13.5 hours of track and before any possible long-term trend had become apparent.

Fish YF8506 (75.25 cm FL) was caught near S FAD at 0630. Unlike the other FAD-associated yellowfin, it immediately began to move steadily away, maintaining a constant southwest course for the next 17.5 hours, at which time the track was terminated (Fig. 5).

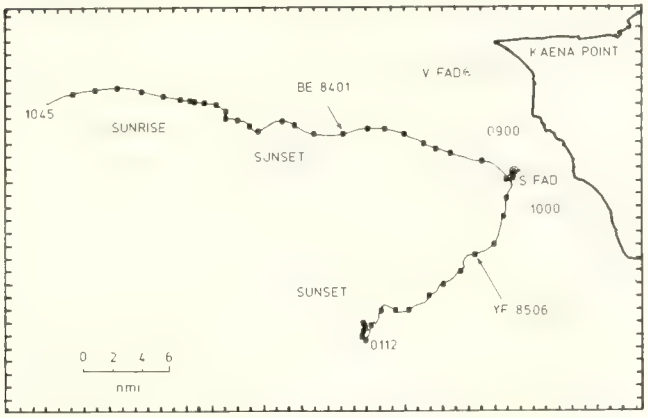

Figure 5

Bigeye BE8401 and yellowfin tuna YF8506 both departed S FAD almost immediately upon release and maintained quite straight azimuths at constant speeds. During darkness, both fish slowed down, and YF8506 became more variable in swimming direction.

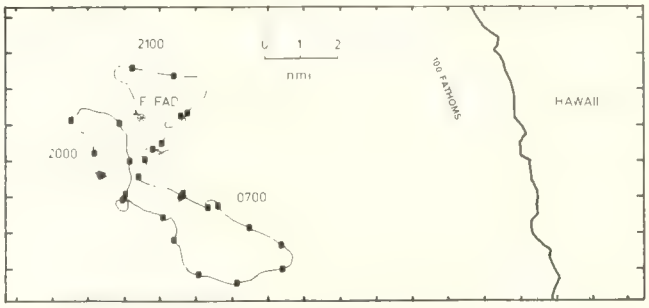

Figure 6

Caught and released after sunset at F FAD off the Kona coast of Hawaii, bigeye tuna BE8205 made a 24-nmi overnight loop before returning to the FAD by late afternoon of the following day.

FAD-associated bigeye tuna Four tracks were made of bigeye tuna caught near FADs. Of these four, one was lost after a few hours and before any diurnal patterns became apparent, one moved continuously away from the FAD (Fig. 5), and two displayed diurnal on-FAD and off-FAD behavior similar to that exhibited by the yellowfin tuna. The following is a synopsis of these two tracks.

Bigeye tuna BE8205 (74.5 cm FL) was caught and tagged 200 m from F FAD off Kona, Hawaii, about 1 hour after sunset (Fig. 6). Upon release, it proceeded on a 24.0-nmi overnight excursion which took it away from the FAD, before gradually reapproaching the FAD in the afternoon of the next day. The maximum distance it moved away from the FAD was 5.75 nmi. This track was then terminated after 24.0 h.

Fish BE8706 (72.0 cm FL) was caught at first light within 50 m of C FAD located off Kealakekua, Hawaii. The fish remained extremely close to the bouy throughout the day until 1 hour after sunset, when it made a 2-nmi excursion that lasted approximately 3 hours. The fish then returned to the immediate vicinity of the buoy, where it remained for the rest of the night and at least through noon of the following day, when the track was terminated after 30.0 hours.

Coastline-associated yellowfin tuna Three tracks were made of yellowfin tuna caught on the reef dropoff on the west coast of Oahu in water between 40 and 50 fathoms (75–95 m) deep. These fish were in the same size range as those caught around the FADs, and tracks spanning 6 days, 36 hours, and 37 hours were obtained, which encompassed a total of six day-night transitions. Two of the three fish displayed offshore excursions every night that they were tracked (a total of five nights). These tracks were as follows.

Fish YF8303 (70.0 cm FL) was caught and tagged at 0855 about 0.75 nmi off the leeward coast of Oahu on the 40-fathom dropoff (Fig. 7A). For the next 7 hours, the fish remained on or near the 40-fathom dropoff, before moving slightly further offshore in the late afternoon. During the subsequent 12 hours of darkness, the fish made a 17-nmi offshore excursion before returning to the 40-fathom contour in the second hour of daylight on the following day. The maximum distance away from the point at which it reencountered the dropoff was approximately 8.25 nmi. The fish remained on the reef slope for the remaining daylight hours until contact was lost at 1130, after 26 hours of tracking.

Forty-eight hours after contact was lost, a hydroacoustic search of the 40-fathom contour reestablished contact with the fish, and the track was resumed at 1426 of the third day (Fig. 7B). The fish spent the remaining daylight hours moving back and forth along the dropoff before moving offshore in late afternoon. The fish spent all night on a 13-nmi excursion before returning to the 40-fathom contour at first light on the next day. The greatest distance from the point of return to the dropoff was approximately 5.25 nmi. The track was suspended at 0730 on the fourth day. The fish was relocated on the 40-fathom isobath on the afternoon of the following (fifth) day at 1642 (Fig. 7C). Again, the fish moved offshore in the late afternoon and spent all night in deeper water on a 7.5 nmi excursion. Maximum distance from the point of return to the dropoff was 3.3 nmi. The time of arrival back at the 40-fathom contour was within 1 minute of the time of arrival on the previous day (Fig. 7B,C). The track was terminated at 0630 on the sixth day because of an impending storm. In summary, this fish was tracked over three day-night-day cycles spanning 6 days and, on each occasion, it made a nighttime off-

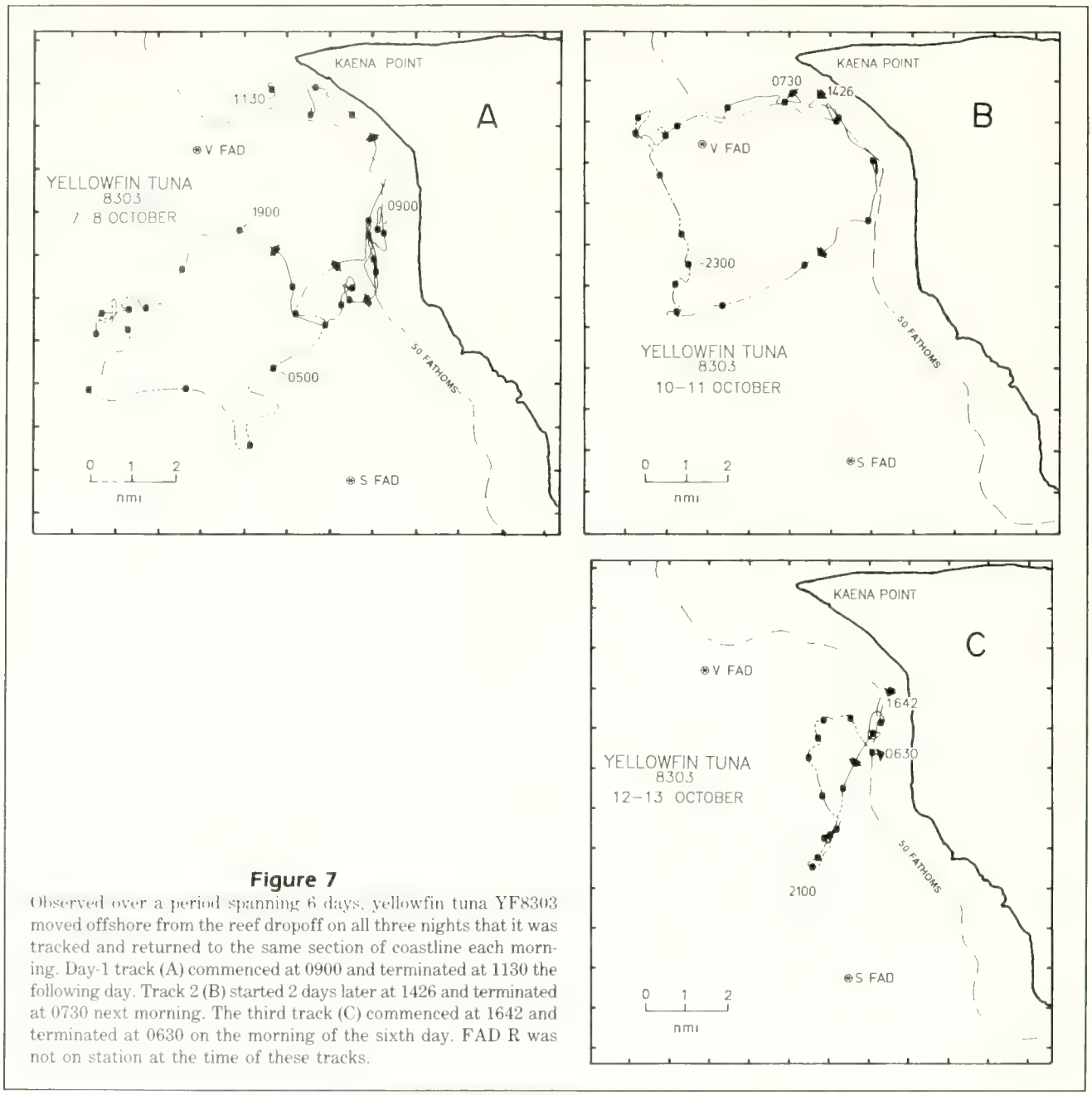

Figure 7

Observed over a period spanning 6 days, yellowfin tuna YF8303 moved offshore from the reef dropoff on all three nights that it was tracked and returned to the same section of coastline each morning. Day-1 track (A) commenced at 0900 and terminated at 1130 the following day. Track 2 (B) started 2 days later at 1426 and terminated at 0730 next morning. The third track (C) commenced at 1642 and terminated at 0630 on the morning of the sixth day. FAD R was not on station at the time of these tracks.

shore excursion followed by a return to the 40-fathom contour on the following morning.

Fish YF8503 (47 cm FL) was caught on the 50-fathom contour at 1200 and stayed in this vicinity for 7.0 hours before moving offshore in the late afternoon to make a 24-nmi nighttime excursion (Fig. 8). The next morning, the fish returned to within 0.5 nmi of the section of coastline it had left the previous evening, the maximum distance from the point of return being 9 nmi. The tracking was temporarily suspended at 0930 and resumed at 1150, when the fish was relocated on the 40-fathom contour near Kaena Point. From here the fish embarked on a prolonged and constant run around the point and along the 40–50 fathom contour of the north shore of Oahu. At sunset of the second day, the fish again moved offshore. When contact was lost at 0100, the fish was 7.5 nmi offshore.

Fish YF8405 (57 cm FL) was caught on the 50-fathom contour and patroled this area for about the next 24 hours. This fish did not move offshore at night. Tracking was suspended at 0715 the second day, but resumed at 1715 the same evening when the fish was

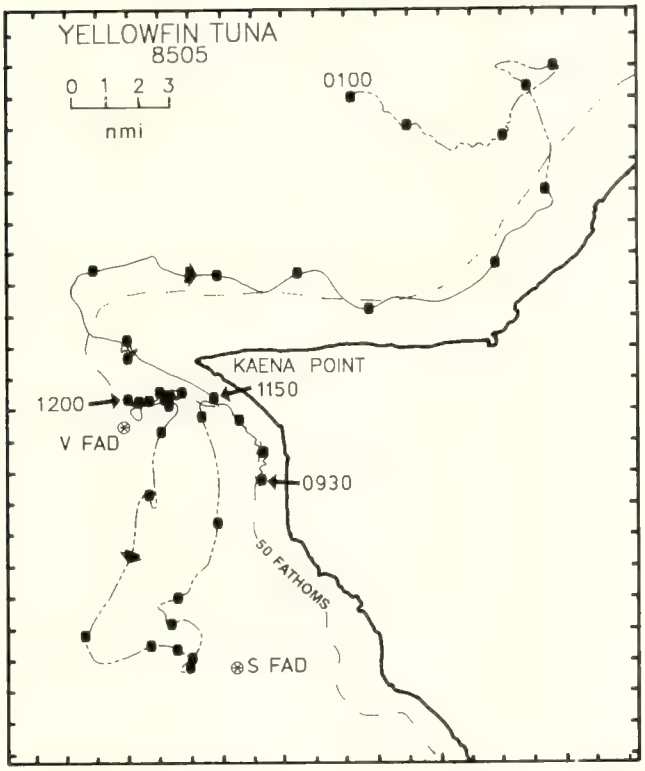

Figure 8

Yellowfin tuna YF8503 moved offshore and made a complete loop during the first night. Tracking was suspended between 0930 and 1150 of the second day. During the second day it swam at a constant pace along the reef dropoff bordering the north shore of Oahu before again heading offshore after sunset on the second night. This demonstrates that the diurnal onshore–offshore pattern is not site-specific to the west coast of Oahu. Contact was lost at 0100.

relocated on the 40-fathom contour. At times, the fish moved into water less than 30 m deep, but was lost just after sunset when the transmitter battery failed. However, this fish was caught two weeks later by a fisherman trolling at R FAD, 7 nmi away from the initial release point.

Combining the FAD-associated and coastline-associated fish, 7 of the 11 yellowfin tuna demonstrated diurnal behavioral patterns in which daytime haunts were abandoned at night. These 7 fish were observed to make a total of 11 nighttime departures from daytime locations. Of those 11 nighttime excursions, 7 were demonstrated to be completed loops wherein the fish returned to their original starting points. In addition, two FAD-associated bigeye tuna completed two nighttime-initiated loops. For the yellowfin tuna, the average maximum distance away from the following morning's destination was 5.28 nmi (SD = 1.9, N = 7). When the two documented bigeye tuna loops are included, the average maximum distance is 4.97 nmi (SD = 2.0, N = 9).

Swimming speeds Unlike the majority of the fish, one bigeye (BE8401) and one yellowfin tuna (YF8506) almost immediately departed their respective FADs and continued to swim away along straight azimuths for the entire duration of the tracks (Fig. 5). Consequently, large sections of these tracks were included in calculations of sustained swimming speeds. Daytime sustained swimming-speed data are summarized in Table 1.

The greatest distance traveled in 1 hour was exhibited at night by YF8503 which traveled 5.0 nmi. This is equivalent to 2.57 m (4.6 body lengths) per second (Fig. 8). When YF8504 was driven away from R FAD by a porpoise school, it swam the first half-hour towards the 40-fathom contour at a rate of 1.32 m (2.4 body lengths) per second (Fig. 3).

Table 1

Daytime sustained swimming speeds of selected yellowfin (YF) and bigeye (BE) tunas.

Track number	Fork length (cm)	Segment duration (h)	Average hourly speed (±SD) m/s	Body lengths (FL)/s
YF8506	72.25	10.0	0.89 ± 0.15	1.19 ± 0.20
YF8502	74.50	7.0	0.95 ± 0.10	1.28 ± 0.14
YF8503	56.00	6.0	1.80 ± 0.38	3.20 ± 0.68
YF8305	54.50	4.0	1.32 ± 0.24	2.40 ± 0.40
		YF Mean =	1.24 ± 0.41	2.01 ± 0.96
BE8401	57.00	13.0	0.79 ± 0.20	1.38 ± 0.35
		Combined mean =	1.15 ± 0.41	1.89 ± 0.88

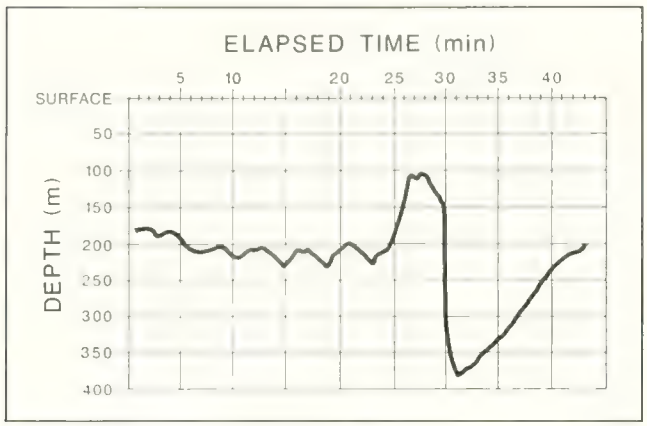

Figure 9

Fine-scale behavior of bigeye tuna BE8401 shown by 45-minute segment of vertical movements transcribed from data tape, including a rapid dive of 230 m in 1 minute, a rate equivalent to 6.7 body lengths/second. Ambient temperature at the maximum depth of 380 m was 9°C.

Vertical movements

The tape recordings of the pulsed signal from the transmitters resulted in detailed, continuous plots of vertical position. Rapid and small-scale changes in depth were discernible (e.g., Fig. 9), as were longer-term diurnal shifts in vertical distribution.

Day-night depth distributions In general, yellowfin tuna swam closer to the surface during darkness. For example, a dramatic change in the depth of swimming of fish YF8305 occurred exactly at sunset and lasted until first light the following morning, when it again began to swim deeper (Fig. 10). Combining all the offshore and off-FAD portions of the yellowfin tuna tracks yielded an average daytime depth of 71.3 m (±42.0 SD, $N = 333$), whereas the average nighttime depth was 47.3 m (±33.1 SD, $N = 444$). These daytime and nighttime depth distributions (Fig. 11A, B) are significantly different (ANOVA, $p = 0.0001$). However, this analysis also indicates significant variability among individual tracks.

Bigeye tuna swam at significantly greater daytime depths than the yellowfin tuna, and showed even greater shifts between daytime and nighttime distributions. When off-FAD, the predominant bigeye tuna daytime distribution was between 220 and 240 m, whereas the predominant nighttime depth was between 70 and 90 m (Fig. 12A, B).

On-FAD versus Off-FAD depth distributions Swimming depths of five yellowfin and one bigeye tuna that were on- and off-FAD during daytime hours support the proposition that FADs tend to bring the fish closer to the surface than they would normally be in other offshore parts of the ocean. These tracks were analyzed to determine if significant changes in depth distribution occurred when the fish were aggregated around the FADs, independant of diurnal influences. When on-FAD, three of the yellowfin tuna were closer to the surface than when off-FAD, one showed no change in depth, and one was deeper. Pooling these data for this subset of yellowfin tuna gave a mean on-FAD depth of 59.3 m (±30.7 SD, $N = 225$), which is significantly different from the mean off-FAD depth of 85.2 m (±52.0 SD, $N = 239$).

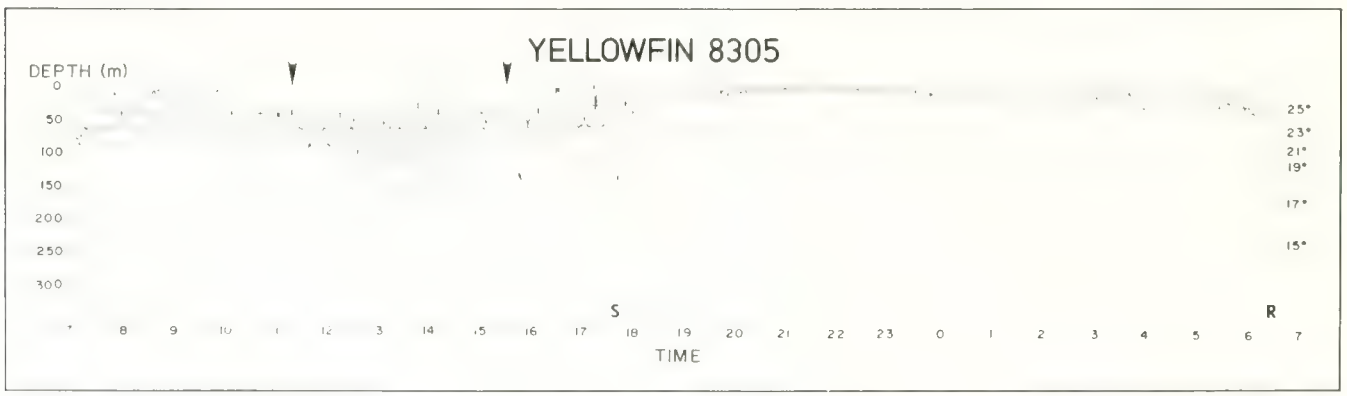

Figure 10

Plot (24-hour) of vertical movements of yellowfin tuna YF8305. In this and subsequent figures, S = sunset, R = sunrise. Arrows denote the beginning and end of time spent at V FAD. Before and after this period, the fish exhibited the "traveling" behavior of making abrupt shifts between the surface and the top layers of the thermocline. Once at the FAD, the vertical behavior became predominantly sinusoidal. All dives made both on- and off-FAD had a consistent floor around 20°C between 140 and 150 m. The rapidly descending trace at end of plot denotes the tag being shed from the fish.

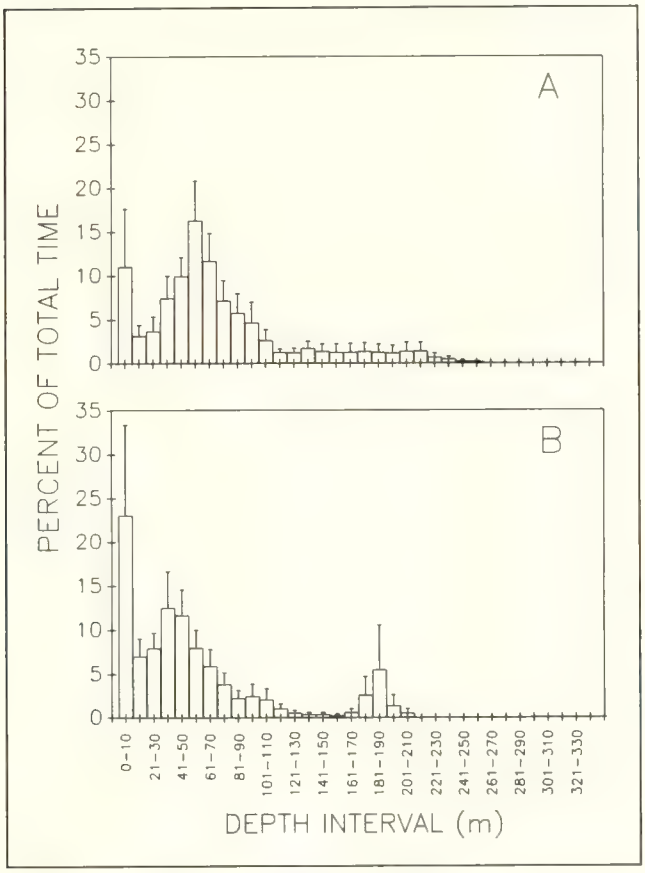

Figure 11

Yellowfin tuna daytime distribution (A) shows two modes, one at the surface and one between 60 and 90 m, which corresponds to the normal position of the interface between the mixed layer and the top layers of the thermocline. Nighttime distribution (B) reflects the tendency of these fish to swim closer to the surface at night. In this and subsequent histograms, bars = standard error.

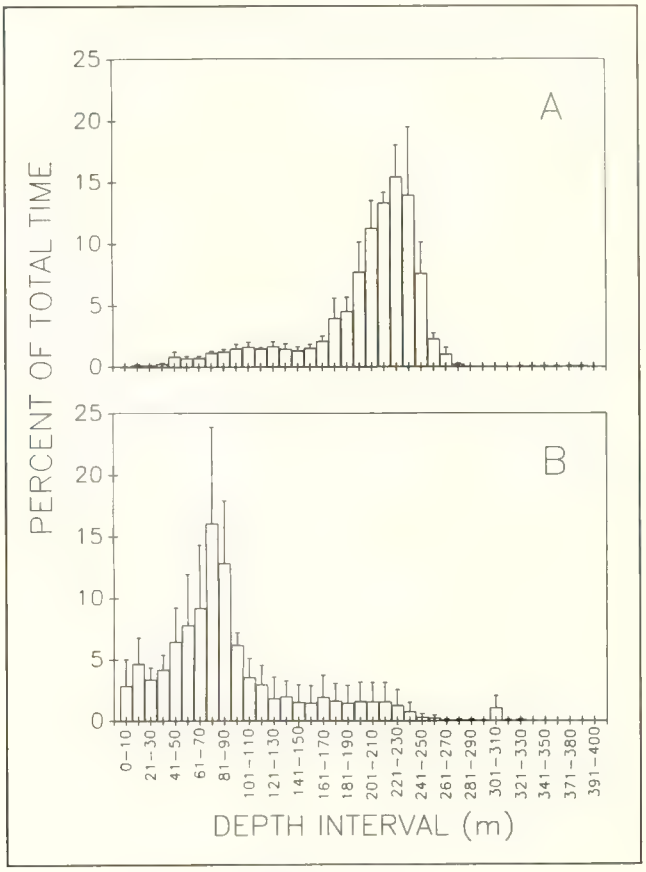

Figure 12

Daytime distribution of bigeye tuna (A) displays a major mode between 200 and 240 m, whereas nighttime distribution is much shallower (B), with the predominant distribution falling between 70 and 90 m.

The tendency of FADs to bring fish closer to the surface was even more apparent in the deeper-swimming bigeye tuna, as was dramatically demonstrated by BE8603 which stayed close to S FAD for 6 hours of daylight before moving away at midday. Figure 13 illustrates the rapid change of depth that coincided with

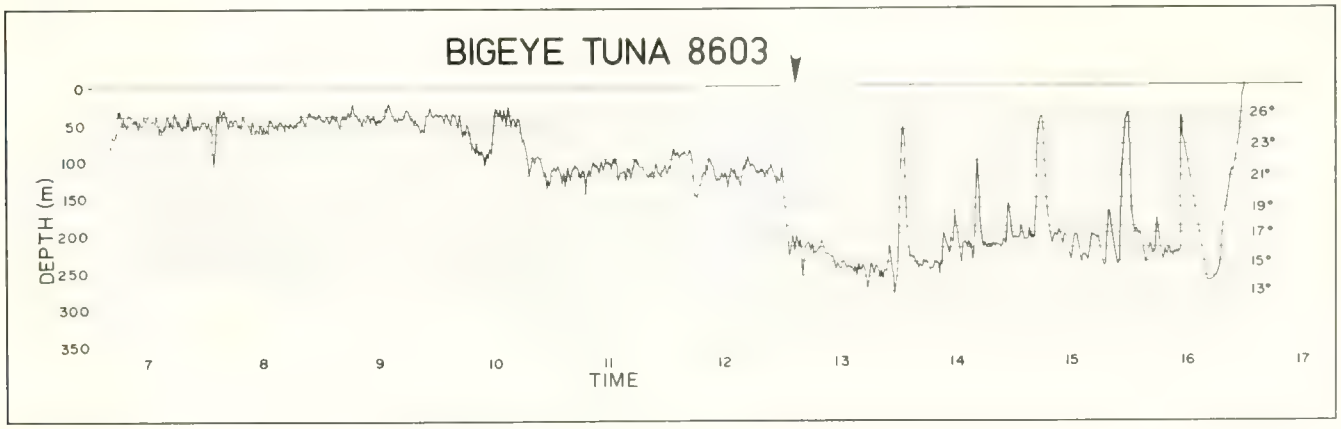

Figure 13

Plot of the on-FAD and off-FAD movements of bigeye tuna BE8603. Arrow indicates when fish departed R FAD.

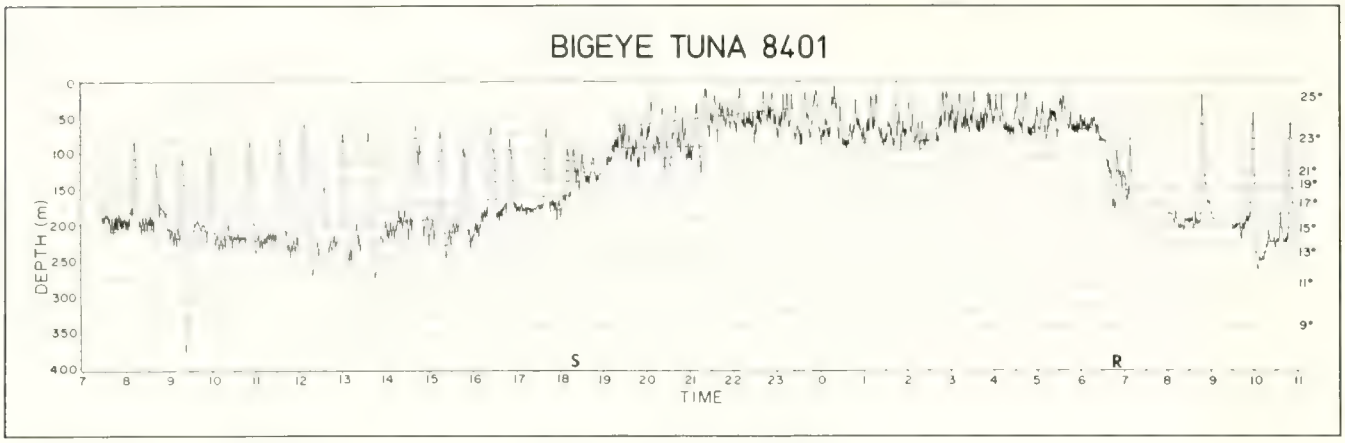

Figure 14
Plot of day-night-day movements of bigeye tuna BE8401. The rapid dive shown in Figure 9 can be seen at 0915 on the first day.

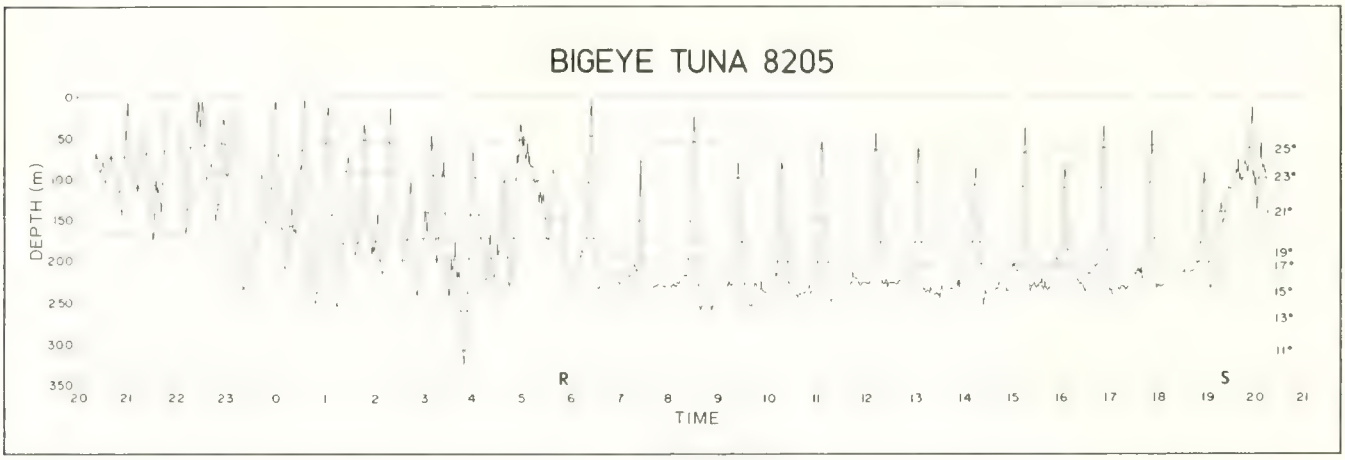

Figure 15
Plot of vertical movements of bigeye tuna BE8205 showing extremely regular daytime upward excursions. These excursions consistently terminated in the zone encompassing the interface between the mixed layer and the thermocline.

the departure of this fish from the FAD. The subsequent depth and pattern of swimming were similar to those shown by the other bigeye tuna that departed their respective FADs almost immediately upon release (Figs. 14, 15). Bigeye tuna BE8706, which remained within 200 m of S FAD for 27.0 hours of the 30.0-hour track, displayed a predominant on-FAD daytime depth of between 50 and 60 m, whereas the predominant, pooled, daytime off-FAD depth of the other three bigeye tuna was 230 m.

Temperature distribution

For the yellowfin tuna, the surface mixed layer (ML) and first degree of the thermocline (ML-1) accounted for 68% of daytime distribution (Fig. 16A). After sunset, the mixed layer alone represented over 62% of the distribution of this species, with the upper 2 degrees of the thermocline contributing an additional 26% of the yellowfin tuna's nighttime distribution (Fig. 16B). Obviously, the warmer nighttime distributions are reflective of the generally shallower depths occupied during the hours of darkness.

In the case of the bigeye tuna, daytime distribution was more dependent on absolute temperature than temperature relative to the surface mixed layer. Thus, in daytime 62.5% of the pooled off-FAD distribution occurred between 14° and 17°C (Fig. 17A). On an individual basis, the strong influence of temperature on daytime vertical distribution was demonstrated by fish BE8401 which consistently oscillated between the 15° and 17°C isotherms even though these isotherms were changing in depth over the course of the track (Fig. 14). Of this bigeye tuna's daytime movements, 68%

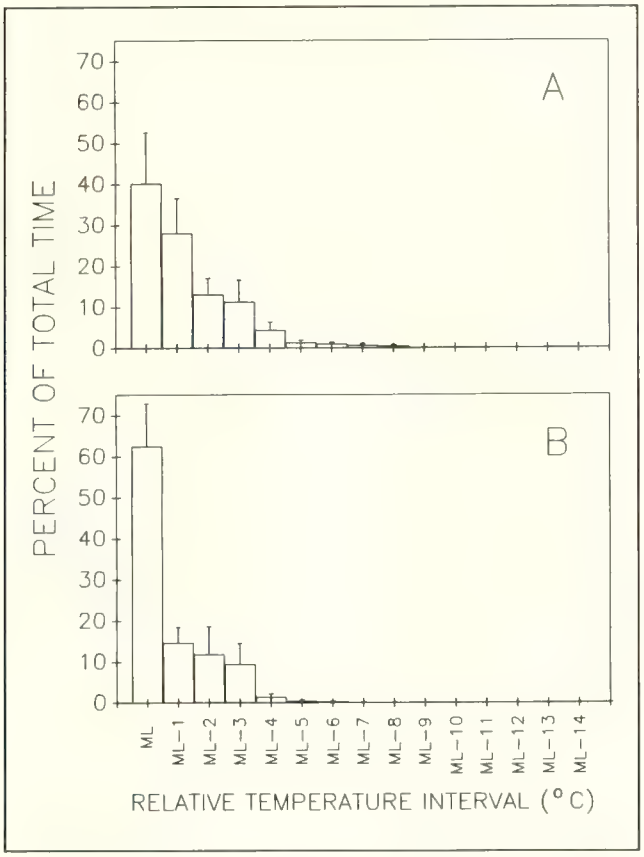

Figure 16
Yellowfin tuna temperature distributions relative to the upper mixed layer (ML). (A) day, (B) night.

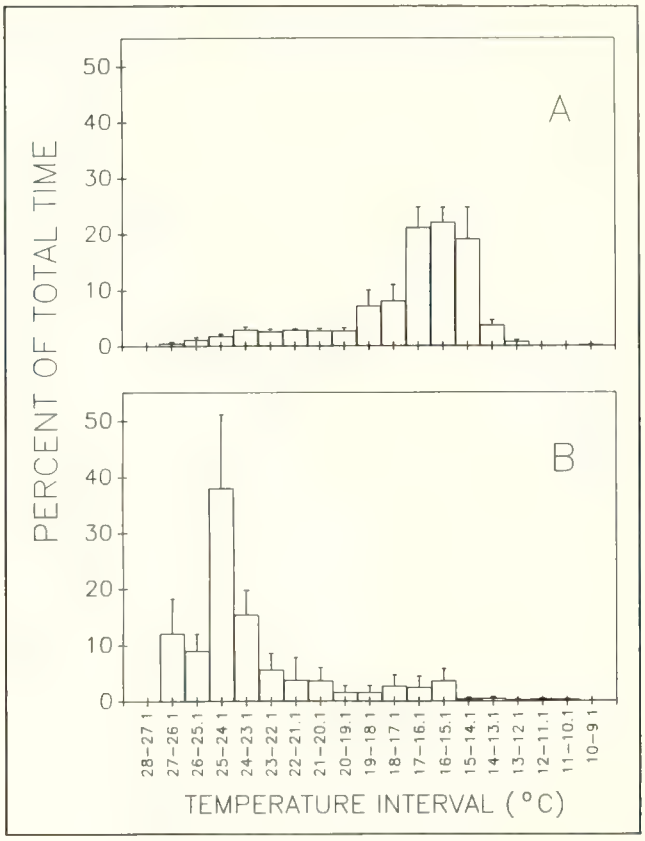

Figure 17
Bigeye tuna temperature distribution. (A) day, (B) night.

occurred between 14° and 17°C. Similarly, BE8205 spent 70% of daylight hours between the 14° and 16°C isotherms (Fig. 15), and BE8603 spent 76% of off-FAD daylight hours between 14° and 17°C isotherms (Fig. 13).

As with the yellowfin, bigeye tuna occupied warmer waters at night (Fig. 17B). The difference between daytime and nighttime temperature distributions was greater for bigeye than for yellowfin tuna because of the much deeper and colder daytime distribution of the bigeye tuna and their comparatively large nocturnal upward shift.

Regular, large, upward excursions were a major feature of the daytime swimming behavior of all the bigeye tuna that were tracked in off-FAD situations (Figs. 13, 14, and 15). This behavior occurred regardless of the type of horizontal movement (e.g., meandering versus straight line). These excursions were comprised of rapid ascents and descents of uniform rate. Ascents usually peaked close to the bottom of the mixed layer and the descending phases usually terminated at the predominant daytime swimming depth. These regular excursions did not occur at night or when on-FAD. For example, these upward excursions were exhibited by fish BE8603 only after it departed S FAD and assumed a deeper off-FAD distribution (Fig. 13). The periodicity and duration of these large excursions were quite regular. For instance, 13 daytime peaks exhibited by BE8205 had a peak-to-peak interval of 57.7 minutes (±7.0 SD) and a duration of 12.0 minutes (±2.6 SD).

Individual fish of both species tended to adopt consistent upper and lower limits to their movements such that, even if they were making frequent upward and downward movements, these were often terminated at consistent depths or temperatures. The most common of these turnaround points was the zone encompassing the bottom of the surface mixed layer and the uppermost layers of the thermocline. Thus, in the case of yellowfin YF8305, the top of the thermocline represented the bottom of dives made from the surface and the starting and finishing points of dives made to deeper depths, most of which had a consistent "floor" around the 20°C isotherm at approximately 130 m (Fig. 10). Similarly, in addition to the well-defined temperature confines of their smaller vertical oscillations, most

of the bigeye tunas' large upward excursions consistently terminated near the interface between the thermocline and the mixed layer (Figs. 13, 14, and 15).

Examples of possible fly-glide behavior (Weihs 1973, Carey and Olsen 1982) were observed in tracks of yellowfin and bigeye tuna, a very consistent example being BE8401, which exhibited "sawtooth" oscillations with a period of approximately 4 minutes and an amplitude between 35 and 45 m for the entire 11-hour daylight segment of the track. Similar, persistent oscillating daytime behavior was exhibited by fish YF8506 as it moved on a direct course away from S FAD (Fig. 18). For instance, between 0930 and 1815 this fish swam on a straight southwesterly course at an apparently constant horizontal speed of 1.02 m/second (Fig. 5). Assuming this constant speed, the descending angles during this period averaged 6.06° (±0.7 SD, $N = 11$), and the climbing angles averaged 9.55° (±1.4 SD, $N = 11$) with 100% of the climbing angles being greater than the descending angles. Also, of the measurable oscillations occurring between 0915 and 1815, 39 out of 46 (85%) displayed longer falling than rising phases, suggesting active upward swimming followed by a comparatively passive downward glide. These oscillations were characterized by constant rates of ascent and descent, with abrupt changes in direction linking the falling and rising phases (Fig. 18).

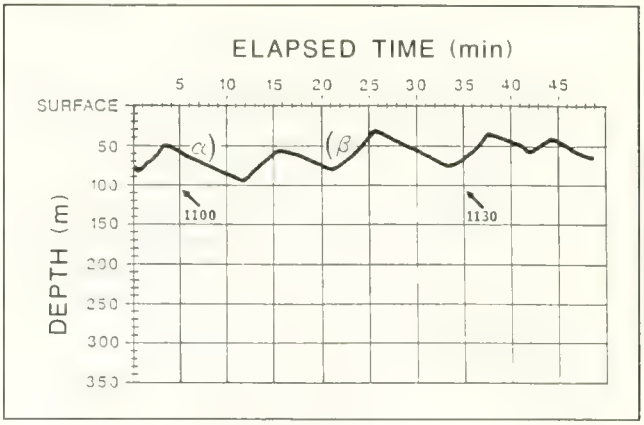

Figure 18

Yellowfin tuna YF8506 showed oscillations suggestive of "fly-glide" behavior while moving on an essentially straight course away from S FAD (cf. Fig. 5). All descending angles (α) were smaller than the climbing angles (β).

Discussion

Using two tie wraps appears to be a satisfactory way of attaching transmitters to tunas. Transmitters attached in this way were carried successfully by four captive fish for several weeks, and one of the tracked fish was caught in good health (and still carrying the transmitter) by a fisherman 2 weeks after we terminated the track. The similarity of vertical and horizontal movements across tracks also suggests minimal alteration of normal behavior.

The association of these tuna with a daytime range, whether FAD or reef perimeter, was extremely strong. In the case of FADs, several fish spent many hours within a few meters of the mooring line. Similarly, none of the reef-associated fish made significant offshore movements during daylight hours. In fact, the alongshore movements were remarkable for their fidelity to the outer reef contour. Combining FAD-associated and reef-perimeter fish, 10 of the 15 fish tracked in this study moved within a well-defined home range during daylight hours and two other fish were lost before any diel patterns could be observed. Most of the fish made nocturnal excursions away from their respective daytime habitats. Similar, consistent diurnal behavior has been previously observed in a 44-cm skipjack tuna, which returned to the same reef after making offshore excursions on each of six nights that it was tracked (Yuen 1970).

This skipjack tuna and the yellowfin tuna tracked in the present study represent the smaller size classes of these species. For fish of these sizes, the reef dropoff probably represents a zone of enhanced prey density where epipelagic species, such as bigeye scad *Decapturus crumenopthalmus*, mackerel scad *D. pinnulatus*, and flying fish (Exocidae), can be found in proximity to reef species which are also prey for these tunas (Hida 1973). The nighttime excursions away from the island reefs and FADs may be foraging behavior targeting on squid and shrimp, which come up from greater daytime depths and which are important components of yellowfin tuna diets (Reintjes and King 1953, King and Ikehara 1956, Brock 1985). Even though the reef-associated fish moved out into deeper water, the nighttime distribution of these yellowfin tuna was closer to the surface than their daytime depths.

The strong daytime association of yellowfin tuna with the FADs, and their nighttime excursions away from them, appears to be analogous to the behavior of island-associated fish patroling the outer reef dropoff. That is, yellowfin tuna appear to respond to FADs as outliers of the natural island topography (e.g., as offshore pinnacles). However, the FAD-associated fish may be paying an energetics penalty because the forage resource at FADs is probably considerably smaller than that available at the reef perimeter. This is indicated by the fact that yellowfin tuna caught at FAD locations have significantly smaller volumes of food in their guts and a significantly higher frequency of completely empty stomachs than do fish caught away from FADs (Brock

1985). Alternatively, it is possible that nighttime feeding excursions away from the FADs, combined with the apparently reduced daytime swimming activity at FADs as compared with reef banks, result in an energetics balance equivalent to that of better-fed, but more active, open-ocean fish or reef-perimeter fish. Even though feeding may not occur as often at FADs as in other areas, FAD-associated tuna may conserve energy normally associated with active hunting. By orienting to FADs, the fish maintain a fixed position in the current flow and may feed on current-borne prey, a situation analogous to trout holding station in a river. The predominant upcurrent orientation of FAD-associated tunas may serve to intercept incoming prey items before they can use the FAD structure for shelter. These feeding advantages would not pertain to tuna associated with logs, which drift with the current and cannot provide the function of serving as a fixed point in a stream. Thus, although logs may indicate areas of enriched forage for planktivores by marking zones of Langmuir cell convergence (Fedoryako 1982), they are unlikely to supply the high food demands of even a medium-sized school of tuna, and, in fact, small fishes found in association with logs are not an important part of the diets of tuna taken from beneath logs (Hunter and Mitchell 1967).

There are other indications that different phenomena may underlie the association of tuna with natural debris and their association with FADs. For instance, fishing techniques which take advantage of log-associated tuna indicate that in these circumstances the tuna tend to aggregate around logs at night and move away in the daytime—exactly the opposite of the behavior observed in the current study. However, in the log situations, tuna behavior may be perturbed by the use of lights placed on the logs by fishermen. Also, since tunas probably are capable of magneticaly mediated orientation (Walker 1984), and in our own study exhibited precise feats of navigation (e.g., returning to the same FAD; navigating between FADs; maintaining straight azimuths over prolonged periods of time), it is unlikely that tunas have trouble distinguishing between logs and FADs because, unlike logs, FADs are both stationary and attached to the ocean floor by visibly (and possibly, acoustically) discernible chain and rope.

The combined data yield an average nightime excursion distance of approximately 5 nmi. This would indicate that to maximize the ability of FADs to aggregate yellowfin tuna consistently, and to minimize the influence of FADs on coastline-associated populations, FADs should be placed a minimum of 5 nmi from the nearest 40-fathom bank. This interpretation is supported by the track of fish YF8504 which rapidly traversed the 3.5 nmi to the 40-fathom contour when disturbed at R FAD by a school of porpoises. Similarly, YF8405 was caught at R FAD 2 weeks after being tracked along the adjacent coastline which, at its nearest point, is between 3.5 and 4.0 nmi away. In fact, optimal FAD placement would be greater than 10 nmi offshore (or from the nearest 40-fathom bank) so that the radii of influence of the FAD and the coastline do not overlap. Frequent anecdotal observations and the impressions of Hawaiian fishermen suggest that FADs located 10 nmi offshore are more consistently productive than FADs located closer to shore.

Daytime orientation of yellowfin tuna to the top layers of the thermocline, with excursions into the mixed layer and to the surface, and a nighttime shallowing into the mixed layer, are consistent with patterns observed by Yonemori (1982) and Carey and Olson (1982). The yellowfin tuna in the current study displayed a particularly strong adherence to the interface between the surface mixed layer and the thermocline when exhibiting straight-line movements. Similar behavior has been previously noted by Carey and Olson (1982). In the present study, these "traveling" fish would often abruptly alternate between the surface and the thermocline interface, both of which might serve to assist straight-line orientation in what is otherwise a truly three-dimensional habitat. By contrast, fish orienting around FADs showed either little vertical movement or vertical movements that were sinusoidal and largely within the mixed layer.

The depth and temperature distributions derived from the bigeye tuna tracks are in good agreement with distributional data obtained by analysis of longline fishing success (Saito 1975; Hanamoto 1976, 1987). These fishery data indicate maximum abundance at depths >200 m and in temperatures between 11° and 15°C, where the dissolved oxygen is >1 mL/L. However, the tracking data suggest daytime distribution (220–240 m, 14–17°C) is influenced at least as much by temperature as by depth, and none of the catch-rate studies indicate the dramatic nighttime upward shift that the tracking data reveal.

The average sustained swimming speed derived from the straight sections of the current yellowfin tuna tracks was 4.46 Km/hour (range 3.2–6.5 Km/hour, Table 1), which is similar to the 4.27 Km/hour average (range 2.4–7.8 Km/hour) reported by Carey and Olson (1982) for fish having an average fork length 41% greater than those used in our study. This comparison would suggest that absolute traveling (sustainable) swimming speed for this species does not increase with size, at least for fish between 45 and 100 cm FL. This constancy of swimming speed, regardless of increasing fish length, is consistent with the model generated by Magnuson (1973, 1978), which predicts that increased weight associated with increasing length is

offset in this species by the allometric growth of the swim bladder, thereby precluding the need to increase hydrodynamic lift through higher swimming speeds. However, the sustained swimming speeds observed during these tracks (average of 1.24 m/second) are considerably higher than the 0.5 to 0.6 m/second predicted by Magnuson (1978) for fish of this size. Obviously, field observations of larger fish would be useful in further testing the Magnuson model.

Periods of possible fly-glide behavior were observed in sections of tracks of yellowfin and bigeye tunas. These oscillations, which in one instance (YF8506) were exhibited for the entire daylight portion of a straight azimuth track, have been hypothesized to result in a saving of energy required for locomotion between two points (Weihs 1973, Magnuson 1978). As predicted by this model, most gliding phases lasted longer than the ascending phases, and the descending and ascending legs were connected by abrupt angles, which maximize energy transfer from the gliding to the flying phase. Thus, using the "fly" angle (β) of 9.55 and "glide" angle (α) of 6.06 obtained from YF8506, and a swim/glide drag ratio (k) of 1.2 (Magnuson 1978), the equation:

$$\text{Energy saving} = 1 - \frac{\tan \alpha}{\sin \beta + (\tan \alpha \cdot \cos \beta)} \times \left(1 + \frac{1 \sin \beta}{k \sin \alpha}\right)$$

results in an energy saving of 9.4% compared with level swimming over the same distance. And, where T is the increased time to travel the same distance using a fly/glide strategy as opposed to level swimming, using the equation

$$T = \frac{\sin \alpha + \sin \beta}{\sin (\alpha + \beta)}$$

indicates that this strategy results in only a 0.9% increase in time to travel the same distance.

The extremely regular, large, upward excursions made by all the off-FAD bigeye tuna during daylight hours may represent behavioral thermoregulation. At the low (14–17°C) ambient temperatures adopted by these fish, their core temperatures possibly drop below some threshold level which requires movement into warmer water to regain optimum body temperatures. If this is the case, it would suggest that there exists a strong motivation for inhabiting the deep cold layers observed during these tracks. A possible motivation would be the opportunity to feed on deepwater fish, squid, and crustaceans which the bigeye tuna then follow into shallower depths at night when these prey organisms migrate toward the surface. Monitoring the core muscle temperatures of bigeye tuna would indicate if, in fact, the large upward excursions are a form of behavioral thermoregulation which, when combined with physiological thermoconservation, allows these fish to exploit an otherwise unreachable resource.

Acknowledgments

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Abstract.– We studied the food habits of the California sea lion *Zalophus californianus* at San Clemente Island, California, from September 1981 through September 1986 using fish otoliths, cephalopod beaks, and other prey remains we recovered from 1476 fecal samples (i.e., scats). We identified 44 types of prey to species and 8 types of prey to genus. Seven types of prey occurred in at least 10% of scats: northern anchovy *Engraulis mordax* (51.3%); jack mackerel *Trachurus symmetricus* (24.6%); pelagic red crab *Pleuroncodes planipes* (21.2%); Pacific whiting *Merluccius productus* (19.6%); rockfishes, *Sebastes* spp. (19.0%); market squid *Loligo opalescens* (16.3%); and blacksmith *Chromis punctipinnis* (10.7%). We examined trends in the occurrence of these seven species and of Pacific mackerel *Scomber japonicus* and octopus (*Octopus* spp.) in scats of California sea lions. We found significant differences among seasons and years, and season-year differences in the occurrence of northern anchovy, jack mackerel, Pacific whiting, and octopus ($P \leq 0.01$). Significant effects due to year and season-year interaction were found for pelagic red crab, rockfish, market squid, and blacksmith. Pacific mackerel showed a significant difference only among years. Significant differences in the occurrence of Pacific whiting, northern anchovy, jack mackerel, Pacific mackerel, market squid, octopus, and pelagic red crab ($P < 0.01$) were found during pre-El Niño, El Niño, and post-El Niño periods.

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Food Habits of California Sea Lions *Zalophus californianus* at San Clemente Island, California, 1981–86

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Knowledge of California sea lion *Zalophus californianus* food habits in the Southern California Bight (SCB, Fig. 1) has come from stomach content analysis by Scheffer and Neff (1948), and Fiscus and Baines (1966); and from the 1978–79 spring and summer study at San Miguel Island from scat (i.e., fecal) analysis by Antonelis et al. (1984). These studies identified a wide variety of prey. Antonelis et al. (1984) reported that Pacific whiting, market squid, juvenile rockfish, and northern anchovy were the four most important prey at San Miguel Island. A 4-year study at the Farallon Islands in northern California (outside the breeding area) found that sea lions switched between Pacific whiting and juvenile rockfish (Bailey and Ainley 1982).

From 1981 to 1986, we examined prey consumed by California sea lions using the shoreline located at and south of Mail Point, San Clemente Island (SCI, Fig. 1). San Clemente Island has one of the smallest rookeries in the SCB (producing approximately 666 pups in 1981) as compared with San Miguel and San Nicolas islands (producing approximately 8255 and 6704 pups, respectively, in 1981; DeMaster et al. 1982, Stewart and Yochem 1984, Oliver and Lowry 1987). We analyzed fecal samples (scats) to identify prey composition and temporal changes in the diet. This period was characterized by an abnormal influx of warm water into the SCB during the 1982–83 El Niño/Southern Oscillation (McGowan 1984). Effects of this El Niño within the SCB became evident in October 1982, when sea-surface temperatures were 1–2°C above normal, and zooplankton levels declined (McGowan 1984). Water temperatures returned to normal in October–November 1984 (F. Miller, Inter-Am. Trop. Tuna Comm., La Jolla, CA 92038, pers. commun., Oct. 1986). This warm-water period off California has been referred to as the California El Niño (McGowan 1984, Fiedler et al. 1986).

Methods

Sample collection

We collected fresh and dry scats during 40 trips to SCI with between-trip intervals ranging from 2 weeks to 3 months. Scats were separated into one of three categories: (1) fresh

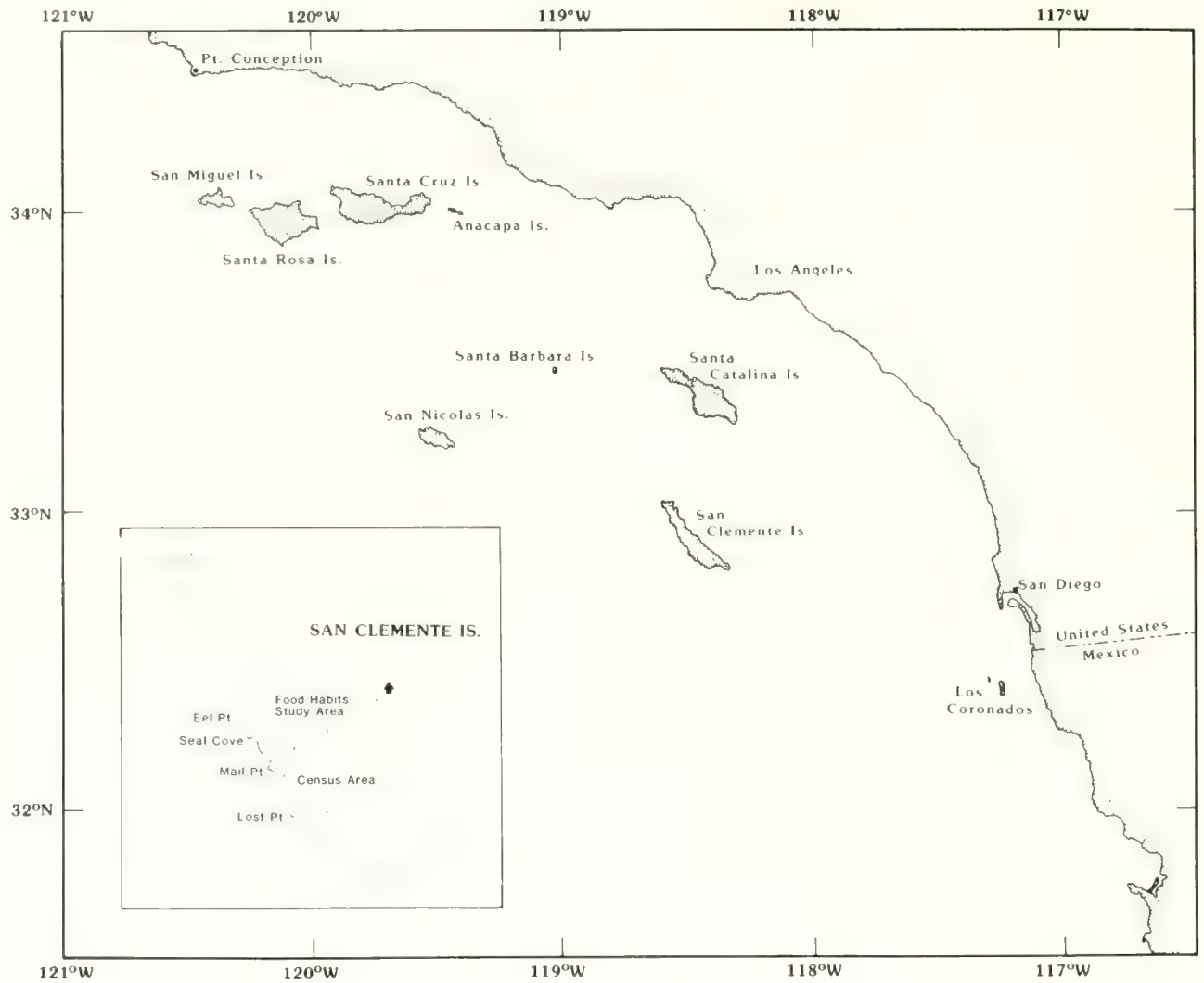


Figure 1
Map showing Southern California Bight (SCB) and San Clemente Island (SCI).

scats, (2) dried scats representing one between-trip interval, and (3) dried scats representing more than one between-trip interval. Fresh scat samples represented the diet of sea lions within 3 to 4 days of the collection. The second category provided dietary information from the previous scat collection period to the time represented by fresh scats. The third category represented a much longer period.

Each scat was placed in a plastic bag, stored in an air-tight plastic container, and frozen until processed. Scats were soaked in a mild soap solution for 1–5 days, and then rinsed with water through two or three nested sieves. During September 1981–March 1983 we used three sieves (mesh sizes 2.8 mm, 1.5 mm, and 1.00 mm) and during April 1983–September 1986 we used two sieves (mesh sizes 2.8 mm and 0.710 mm). After rinsing, we collected fish otoliths, cephalopod beaks, shark teeth, and cartilaginous vertebrae. Otoliths, shark teeth, and cartilaginous vertebrae were air dried and stored in gelatin capsules; cephalopod beaks were stored in vials containing 70% ethanol. We noted the presence or absence of fragments of pelagic red crabs *Pleuroncodes planipes*.

Sample analysis

Prey items were identified to the lowest taxon possible from comparative specimens and drawings (Iverson and Pinkas 1971, Eschmeyer et al. 1983). We used sagittal otoliths to identify teleost fishes, cephalopod beaks to identify squid and octopus, teeth to identify elasmobranchs, and exoskeletal fragments to identify pelagic red crabs. We counted left and right sagittal otoliths, and upper and lower cephalopod beaks.

Table 1

California sea lion *Zalophus californianus* scat samples collected seasonally from San Clemente Island, California, 1981–86.

Year	Season	Number of collection trips	Number of scats collected			
			Fresh	Dry		Total collected
				1 between-trip interval	>1 between-trip interval	
1981	Autumn	3	22	19	7	48
1981–82	Winter	1	0	3	0	3
1982	Spring	4	27	80	52	159
1982	Summer	4	76	67	7	150
1982	Autumn	1	1	53	0	54
1982–83	Winter	2	3	56	0	59
1983	Spring	3	37	73	60	170
1983	Summer	2	6	71	10	87
1983	Autumn	1	22	56	17	95
1983–84	Winter	3	93	51	4	148
1984	Spring	2	81	20	16	117
1984	Summer	3	88	1	0	89
1984	Autumn	2	13	40	0	53
1984–85	Winter	1	0	16	0	16
1985	Spring	1	11	1	0	12
1985	Summer	2	60	0	0	60
1985	Autumn	1	25	0	0	25
1986	Spring	1	44	0	0	44
1986	Summer	2	65	0	0	65
1986	Autumn	1	22	0	0	22
Total		40	696	607	173	1476

We used indices of occurrence, composition, and number to quantify prey taxon consumed by sea lions. Only scat samples containing otoliths, cephalopod beaks, shark teeth, cartilaginous vertebrae, or pelagic red crab fragments were used in the analysis. The occurrence index, or percent occurrence (PO), is a measure of the percentage of scat samples in which a prey taxon occurred. The composition index, or percent prey composition (PPC), is a measure of the percentage of occurrences for each prey taxon from a tally of occurrences from all prey taxa found in a group of samples. The number index, or percent minimum number (PMN), measures the percentage of numbers of individual prey taxon. To compute the number index, we used the maximum count of either left or right otoliths, or upper or lower beaks, which represent the minimum number of individual prey taxon. The counts for all prey taxa are summed and the percentage of each prey taxon is determined from the sum of all counts. The number index is, then, the percentage represented by each prey taxon from the sum of all maximum counts taken of all prey taxa found in a group of samples.

Interpretation of the number index is limited because it excludes (1) all prey hard parts found that were broken or digested, and not categorized as either left or right otoliths or upper or lower beaks, and (2) prey that lacked otoliths or beaks (e.g., pelagic red crabs and sharks). However, we think that this index is useful because fish and cephalopods represented the majority of prey in scat samples.

Percent occurrence indicates prey consumption without regard to other prey, and may indicate temporal availability, selectivity, or ease of capture of individual prey. Percent prey composition indicates the relative proportions of prey consumed. Percent minimum number of prey indicates numbers of prey consumed and is an index of the rate of consumption of individual prey.

Statistical analysis

We used all scats to determine what prey taxa were consumed, and then limited our examination of temporal variations in prey consumption to prey that occurred in at least 10% of these scats, were found in at least 80% of the seasons, or were occasionally very abundant. Only fresh scats and dried scats representing one between-trip interval were used in the temporal analyses of sea lion diets. We combined the 40 collection trips (Table 1) by season into winter (December–

Table 2

Number of prey occurrences (*n* Occur), percent occurrence (PO), percent prey composition (PPC), minimum number of individual prey (*n* Ind.), and percent minimum number (PMN) of prey found in 1309 California sea lion scats collected at San Clemente Island, California, 1981–86.

Prey						
Scientific name	Common name	*n* Occur	PO	PPC	*n* Ind.	PMN
Engraulis mordax	northern anchovy	672	51.3	24.7	9,398	54.4
Trachurus symmetricus	jack mackerel	322	24.6	11.8	1,220	7.1
*Pleuroncodes planipes**	pelagic red crab	277	21.2	10.2	–**	–
Merluccius productus	Pacific whiting	256	19.6	9.4	2,110	12.2
Sebastes spp.	rockfish	249	19.0	9.2	1,245	7.2
Loligo opalescens	market squid	214	16.3	7.9	1,516	8.8
*Chromis punctipinnis**	blacksmith	140	10.7	5.1	580	3.4
Scomber japonicus	Pacific mackerel	125	9.5	4.6	215	1.2
Octopus spp.	octopus	67	5.1	2.5	523	3.0
Onychoteuthis borealijaponicus	squid	39	2.2	1.1	33	<0.5
Lyopsetta exilis	slender sole	11	0.8	<0.5	19	<0.5
*Oxyjulis californica**	señorita	14	1.1	0.5	20	<0.5
Porichthys notatus	plainfin midshipman	9	0.7	<0.5	11	<0.5
Abraliopsis spp.*	squid	9	0.7	<0.5	11	<0.5
Gonatus spp.	squid	9	0.7	<0.5	11	<0.5
*Lycodes cortezianus**	bigfin eelpout	7	0.5	<0.5	8	<0.5
*Sebastolobus alascanus**	shortspine thornyhead	6	0.5	<0.5	7	<0.5
Microstomus pacificus	dover sole	6	0.5	<0.5	8	<0.5
Glyptocephalus zachirus	rex sole	6	0.5	<0.5	7	<0.5
Icichthys lockingtoni	medusafish	5	<0.5	<0.5	7	<0.5
*Xeneretmus ritteri**	stripefin poacher	3	<0.5	<0.5	5	<0.5
Citharichthys sordidus	Pacific sanddab	4	<0.5	<0.5	5	<0.5
*Atherinops affinis**	topsmelt	3	<0.5	<0.5	4	<0.5
*Semicossyphus pulcher**	sheephead	3	<0.5	<0.5	3	<0.5
Seriphus politus	queenfish	2	<0.5	<0.5	26	<0.5
*Cypselurus californicus**	California flying fish	2	<0.5	<0.5	8	<0.5
Genyonemus lineatus	white croaker	2	<0.5	<0.5	6	<0.5
*Galeorhinus zyopterus**	soupfin shark	2	<0.5	<0.5	–	–
Symbolophorus californiensis	California lanternfish	2	<0.5	<0.5	2	<0.5
*Paralabrax clathratus**	kelp bass	2	<0.5	<0.5	2	<0.5
Chilara taylori	spotted cusk-eel	2	<0.5	<0.5	2	<0.5
Cymmatogaster aggregata	shiner surfperch	2	<0.5	<0.5	2	<0.5
Stenobrachius leucopsarus	northern lampfish	2	<0.5	<0.5	2	<0.5
Paralabrax sp.*	seabass	1	<0.5	<0.5	3	<0.5
*Octhoe tuberculata**	squid	1	<0.5	<0.5	2	<0.5
Girella nigricans	opaleye	1	<0.5	<0.5	2	<0.5
Zalembius rosaceus	pink surfperch	1	<0.5	<0.5	1	<0.5
Zaniolepis sp.*	combfish	1	<0.5	<0.5	1	<0.5
Xeneretmus sp.*	poacher	1	<0.5	<0.5	1	<0.5
*Prionace glauca**	blue shark	1	<0.5	<0.5	–	–
*Argentina sialis**	Pacific argentine	1	<0.5	<0.5	1	<0.5
*Hippoglossina stomata**	bigmouth sole	1	<0.5	<0.5	1	<0.5
Parophrys vetulus	english sole	1	<0.5	<0.5	1	<0.5
*Xeneretmus triacanthus**	bluespotted poacher	1	<0.5	<0.5	1	<0.5
*Ceratoscopelus townsendi**	dogtooth lampfish	1	<0.5	<0.5	4	<0.5
Citharichthys sp.	sanddab	1	<0.5	<0.5	1	<0.5
*Careproctus melanurus**	blacktail snailfish	1	<0.5	<0.5	1	<0.5
*Medialuna californiensis**	halfmoon	1	<0.5	<0.5	3	<0.5
*Synodus lucioceps**	California lizardfish	1	<0.5	<0.5	1	<0.5
*Octopoteuthis deletron**	squid	1	<0.5	<0.5	1	<0.5
Unid. Myctophidae	lanternfish	17	1.3	0.6	29	<0.5
Unid. Embiotocidae	surfperch	4	<0.5	<0.5	7	<0.5
Unid. Atherinidae	silverside	3	<0.5	<0.5	3	<0.5
Unid. Labridae	wrasse	3	<0.5	<0.5	8	<0.5
Unid. Cottidae	sculpin	2	<0.5	<0.5	2	<0.5
Unid. Zoarcidae	eelpout	2	<0.5	<0.5	2	<0.5

Table 2 (continued)

Prey						
Scientific name	Common name	*n* Occur	PO	PPC	*n* Ind.	PMN
Unid. Gonatidae	squid	1	<0.5	<0.5	1	<0.5
Unid. Scombridae	mackerel or tuna	1	<0.5	<0.5	2	<0.5
	Unid. flatfish	5	<0.5	<0.5	6	<0.5
	Unid. cephalopod	31	2.4	1.1	19	<0.5
	Unid. cartilaginous fish	2	<0.5	<0.5	–	–
	Unid. fishes	83	6.3	3.1	62	<0.5

*Not previously reported as prey of California sea lions.
**Data impossible to compute in fields marked with a dash (–).

February), spring (March–May), summer (June–August), and autumn (September–November). We also categorized our sample into three groups related to the California El Niño: (1) pre-El Niño (September 1981–August 1982), (2) El Niño (November 1982–September 1984), and (3) post-El Niño (November 1984–September 1986).

We tested for seasonal and yearly differences in presence or absence of each prey taxon using two-way ANOVA (Program 7D of BMDP-87; Dixon 1985) in the binomial format. Two data sets were identified with full cells in order to meet the requirements of the test: (1) all seasons for the years 1982–85 (called four-season-four-year data set); and (2) three seasons (spring, summer, and autumn) for 1982–86 (called three-season-five-year data set). We identified prey taxa that showed significant season, year, and season-year interaction differences in their occurrence through time using Browne-Forsythe analysis of variance for unequal variances. For the pre-El Niño, El Niño, and post-El Niño comparisons, we tested for differences in presence or absence of the same nine prey taxa using two-way Browne-Forsythe ANOVA (Dixon 1985) in the binomial format.

We also examined temporal differences in the relative number of different prey taxa found per scat (1, 2, 3, 4, 5, or >5). Pearson's chi-square test (Dixon 1985) was used to test for differences among numbers of prey occurring per scat.

Results

Identification of prey remains

In the 1476 scats collected (Table 1), we found the following: (1) 1455 scats (98.5%) contained fish remains (i.e., bones, otoliths, or eye lenses); (2) 525 scats (35.5%) contained cephalopod remains (i.e., beaks or eye lenses); (3) 1309 scats (88.6%) contained fish otoliths, cephalopod beaks, or other prey remains that were used to identify prey; (4) 1271 scats (86.1%) contained fish otoliths; and (5) 344 scats (23.3%) contained cephalopod beaks.

We identified 95.4% of 2647 prey occurrences to species, genus, or family (Table 2). Of the 2,647 prey occurrences, 75.2% were bony fishes, 14.1% were cephalopod, 10.5% were crustacea (99.3% of crustacea were pelagic red crab), and 0.2% were cartilaginous fish. We identified 44 prey taxa to species level and 8 to genus level. Seven prey taxa occurred in >10% of scats: northern anchovy *Engraulis mordax* (51.3%); jack mackerel *Trachurus symmetricus* (24.6%); pelagic red crab *Pleuroncodes planipes* (21.2%); Pacific whiting *Merluccius productus* (19.6%); rockfishes, *Sebastes* spp. (19.0%); market squid *Loligo opalescens* (16.3%); and blacksmith *Chromis punctipinnis* (10.7%). Two prey taxa occurred in 5.0–10.0% of the scats: Pacific mackerel *Scomber japonicus* (9.5%) and octopus, *Octopus* spp. (5.1%). We identified 17 species and two genera of fish, and two species and one genus of cephalopod not reported previously as prey of California sea lions (Table 2).

Nearly half of the scats (46.1%) contained only one prey taxa (Fig. 2). Northern anchovy constituted 56.2% of 603 scat samples with single prey taxa (Fig. 3).

Variability in diet through time

We found differences in distributions of occurrence (occurrence and composition indices) and numbers of individuals (number index) for nine prey taxa examined for temporal variability during the pre-El Niño, El Niño, and post-El Niño periods (Fig. 4). The distributions of occurrence were significantly different for Pacific whiting, northern anchovy, jack mackerel, Pacific mackerel, market squid, octopus and pelagic red crab ($P<0.01$). Northern anchovy occurred frequently and in the highest numbers of any prey taxa in all three periods. During the pre-El Niño period, jack mackerel occurred in the scat samples more often than the other prey; and jack mackerel and market squid were found in greater indi-

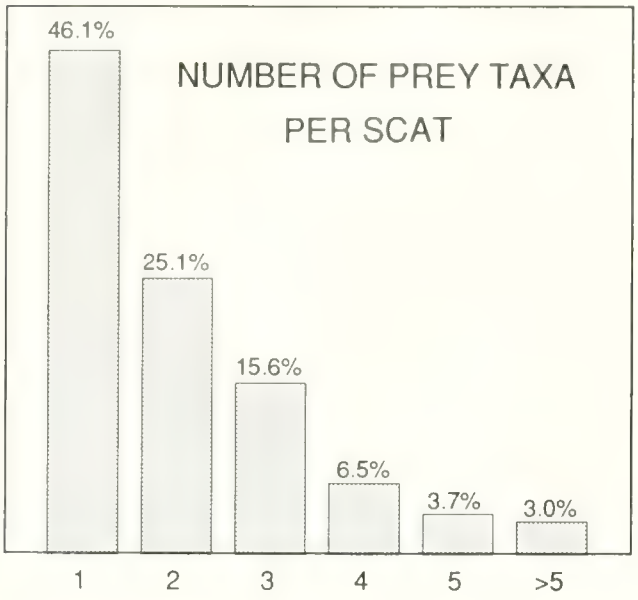


Figure 2

Occurrence of single and multiple prey taxa in 1309 California sea lion scats collected at San Clemente Island, California.

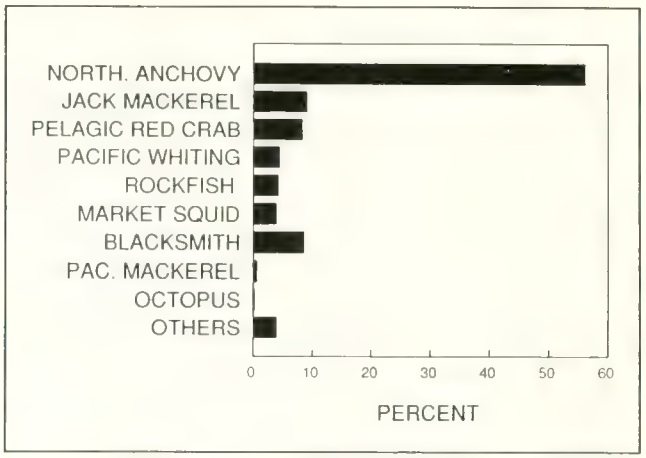
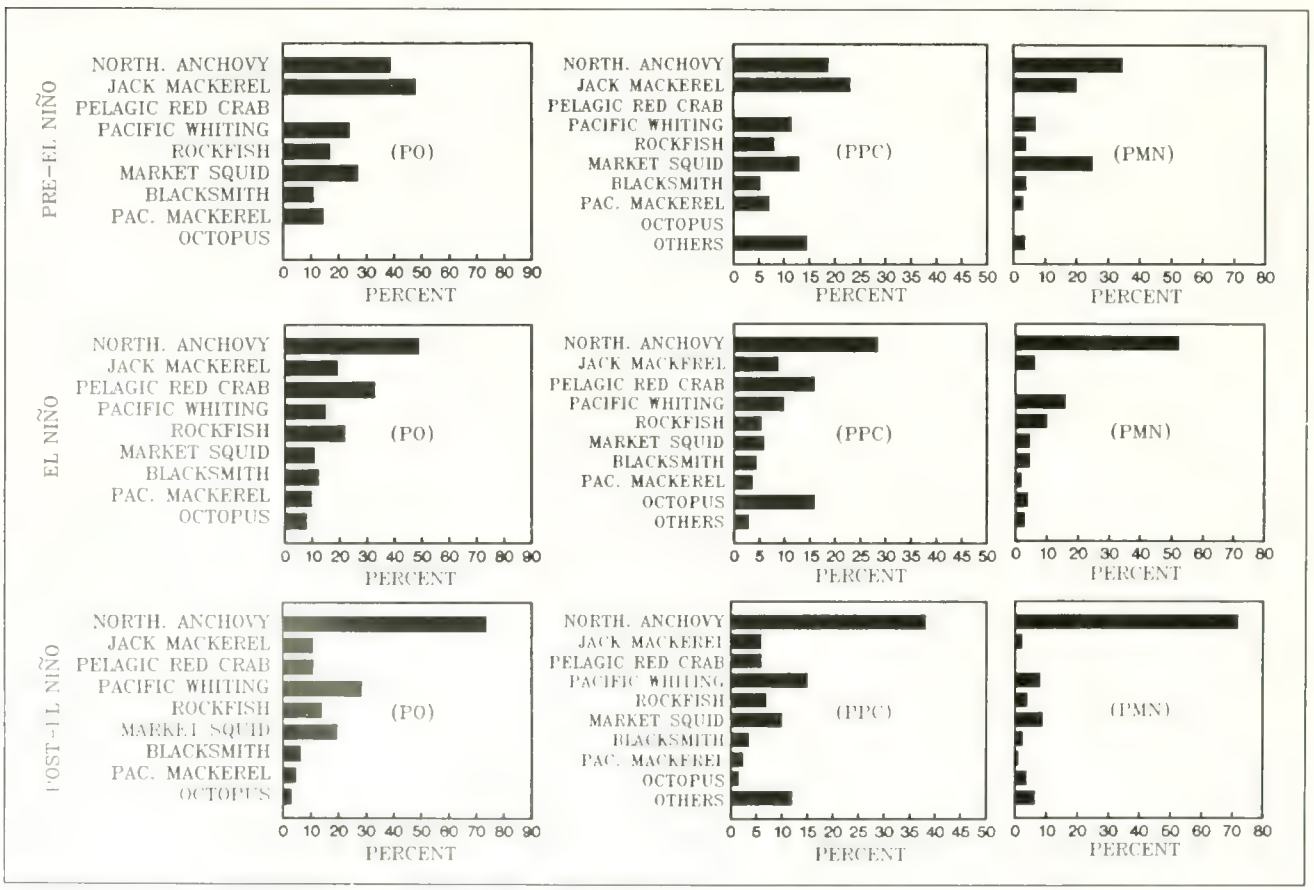


Figure 3

Percent prey found in 603 California sea lion scats with single prey taxon.

Figure 4

Occurrence (PO), composition (PPC), and number (PMN) indices of 9 prey taxa found in 1309 California sea lion scats collected at San Clemente Island, California, 1981–86, which are divided into pre-El Niño (September 1981–August 1982), El Niño (November 1982–September 1984), and post-El Niño (November 1984–September 1986) periods. The number index (PMN) could not be determined from fragments of pelagic red crab.



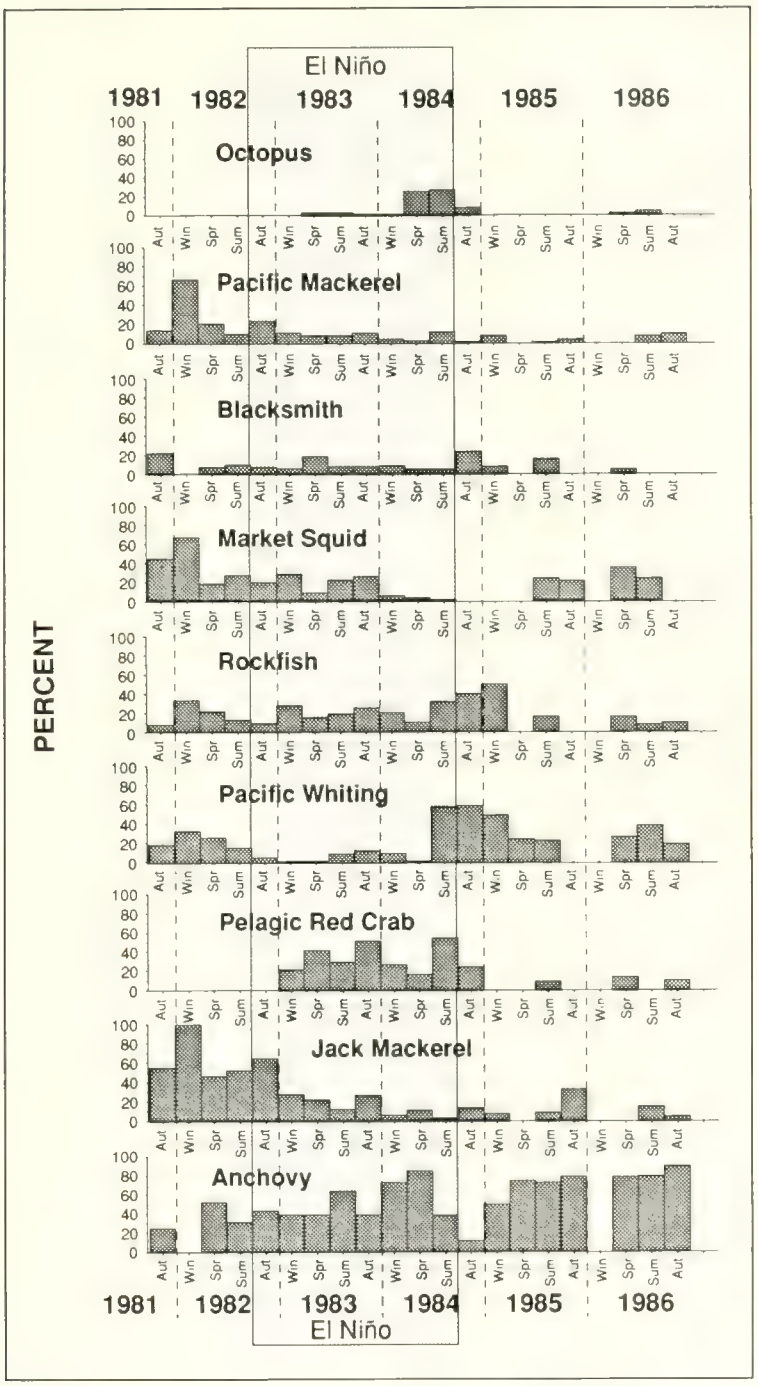


Figure 5
Seasonal percent occurrence (PO) of 9 prey taxa found in 1304 California sea lion scats, 1981–86. No samples were collected in winter 1986.

vidual numbers than other prey taxa, except northern anchovy. During the El Niño period, pelagic red crab were the second most frequently occurring prey in scat samples. During the post-El Niño period, the diet was dominated by northern anchovy.

We found yearly and seasonal variability in the relative proportions represented by the three indices for 9 prey taxa examined (Figs. 5–7). Northern anchovy was consistently found in scats throughout the study at varying occurrence, composition, and number index levels. However, during summer and autumn 1984 we noted a drop in the three indices compared with 1982, 1983, 1985, and 1986; and it did not occur as often in 1982 as in 1983, 1985, and 1986. Jack mackerel was the most frequent prey during 1981–82, but after that period it was found infrequently, represented a very small proportion of the diet, and few individuals were found in the scats. An increase in the occurrence of

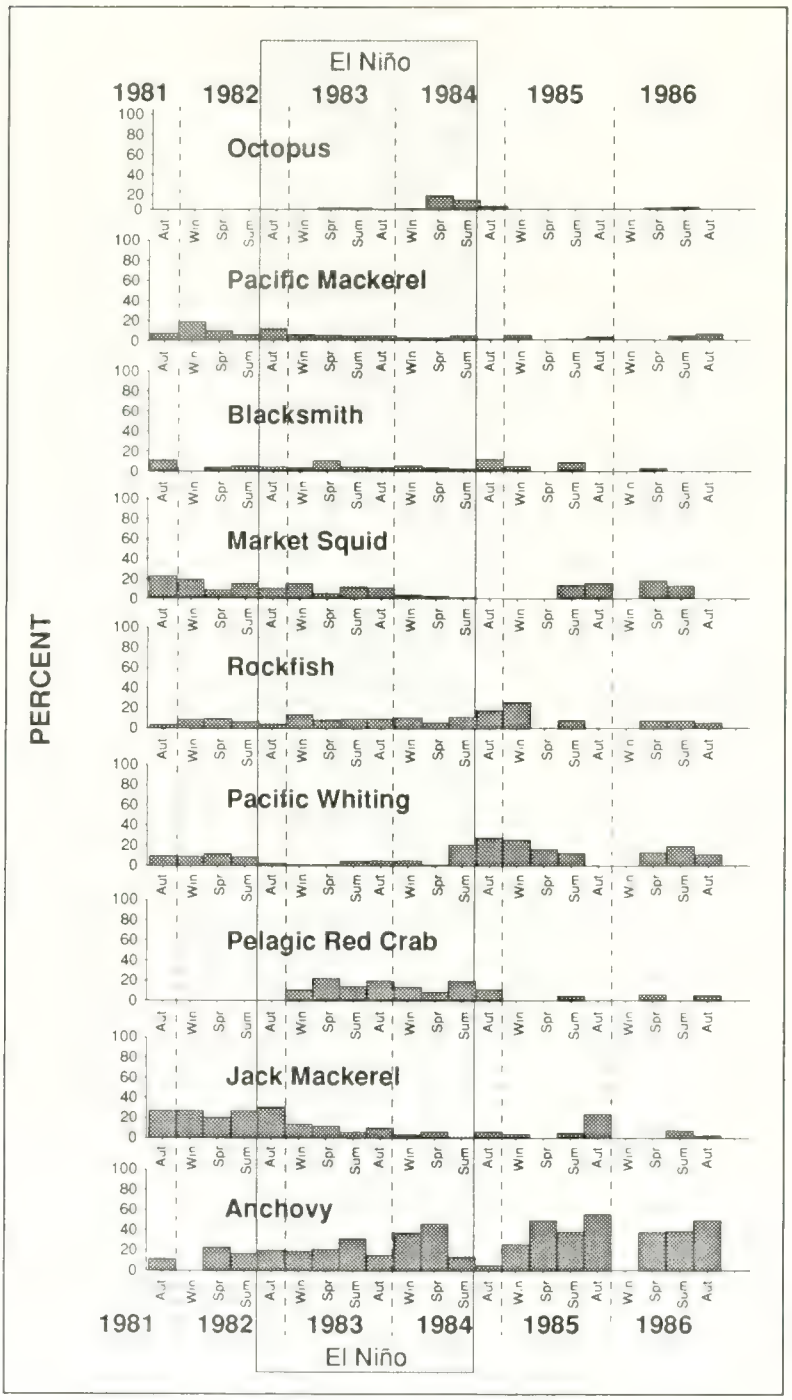


Figure 6

Seasonal percent prey composition (PPC) of 9 prey taxa found in 1304 California sea lion scats, 1981–86. No samples were collected in winter 1986.

Pacific whiting was found during summer–autumn 1984 and winter 1985 when many individuals were found in scats. Rockfish was consistently found in scats throughout the study, but more individuals were represented during summer–autumn 1984 and winter 1985 than other times. Market squid was found in extremely low occurrence, composition, and number index levels ($\leq$5.6%) or was absent from scat samples from winter 1984 through spring 1985. Pelagic red crab occurred primarily during the 1983–84 California El Niño period. Pacific mackerel occurred in the scat samples more often in 1982 than during the following years, but was represented by few individuals from 1981 to 1986. Blacksmith occurred in scat samples throughout the 1981–84 period, but during the 1985–86 period it occurred inconsistently in the diet. Octopus appeared in the samples from spring 1983 to autumn 1984, and spring–summer 1986.

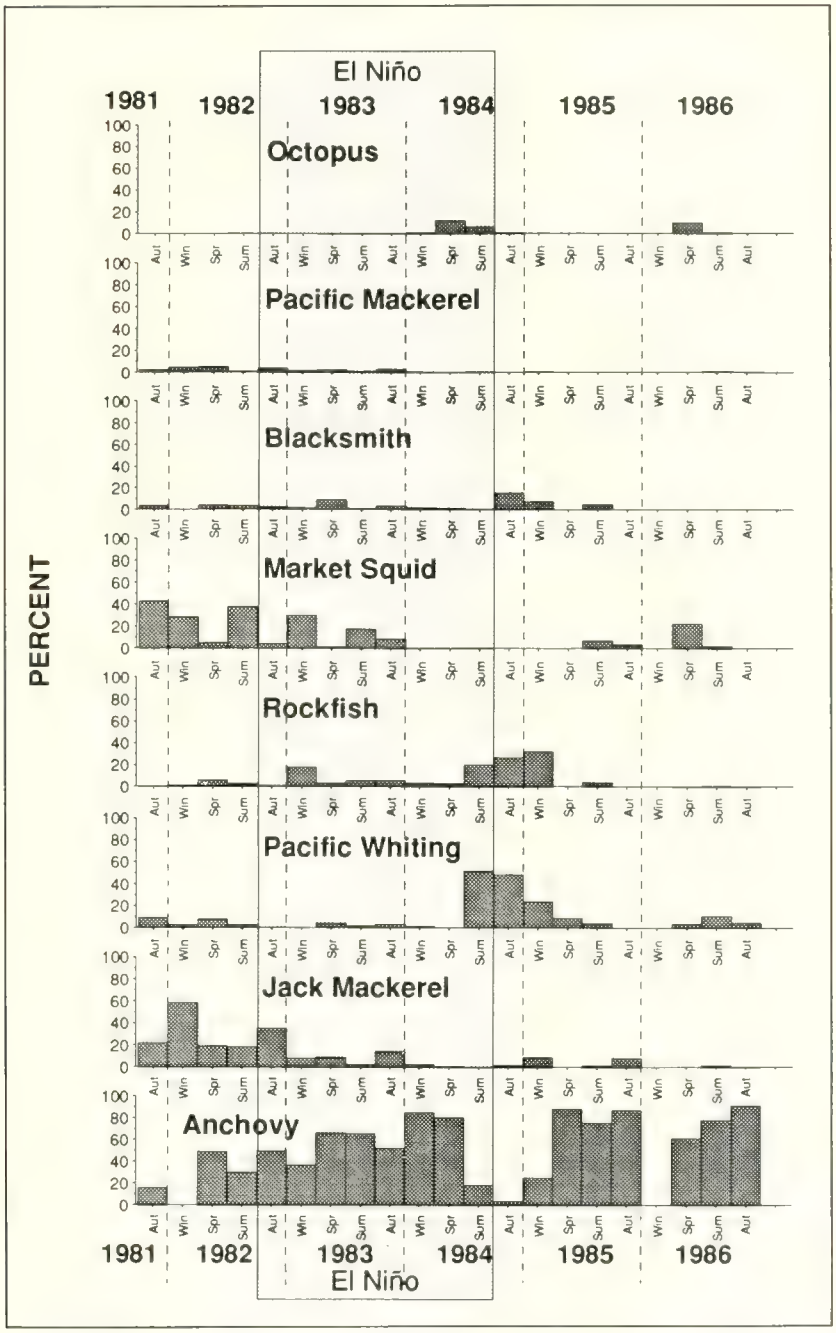


Figure 7

Seasonal percent minimum number (PMN) of 8 prey taxa found in 1304 California sea lion scats, 1981–86. No samples were collected in winter 1986. PMN could not be determined from fragments of pelagic red crab.

Analyses of the three-season-five-year and four-season-four-year data sets indicated significant differences ($P \leq 0.05$) in the occurrence of some, but not all, of the nine prey tested. Variances of occurrence were significantly different for all nine prey (Levene's test, $P \leq 0.05$). The three-season-five-year data set showed 21 significant differences in year, season, or season-year interactions, and the four-season-four-year data set showed 14 significant differences in year, season, or season-year interactions. Because the three-season-five-year data set included more of the post-El Niño period, results from that data set were used to interpret seasonal and yearly changes in prey items. Northern anchovy, jack mackerel, Pacific whiting, and octopus showed significant seasonal, yearly, and season-year interaction differences ($P<0.01$). Pelagic red crab, rockfish, market squid, and blacksmith showed only significant yearly and season-year interactions differences ($P<0.01$). Pacific mackerel had a significant difference only among years ($P<0.01$).

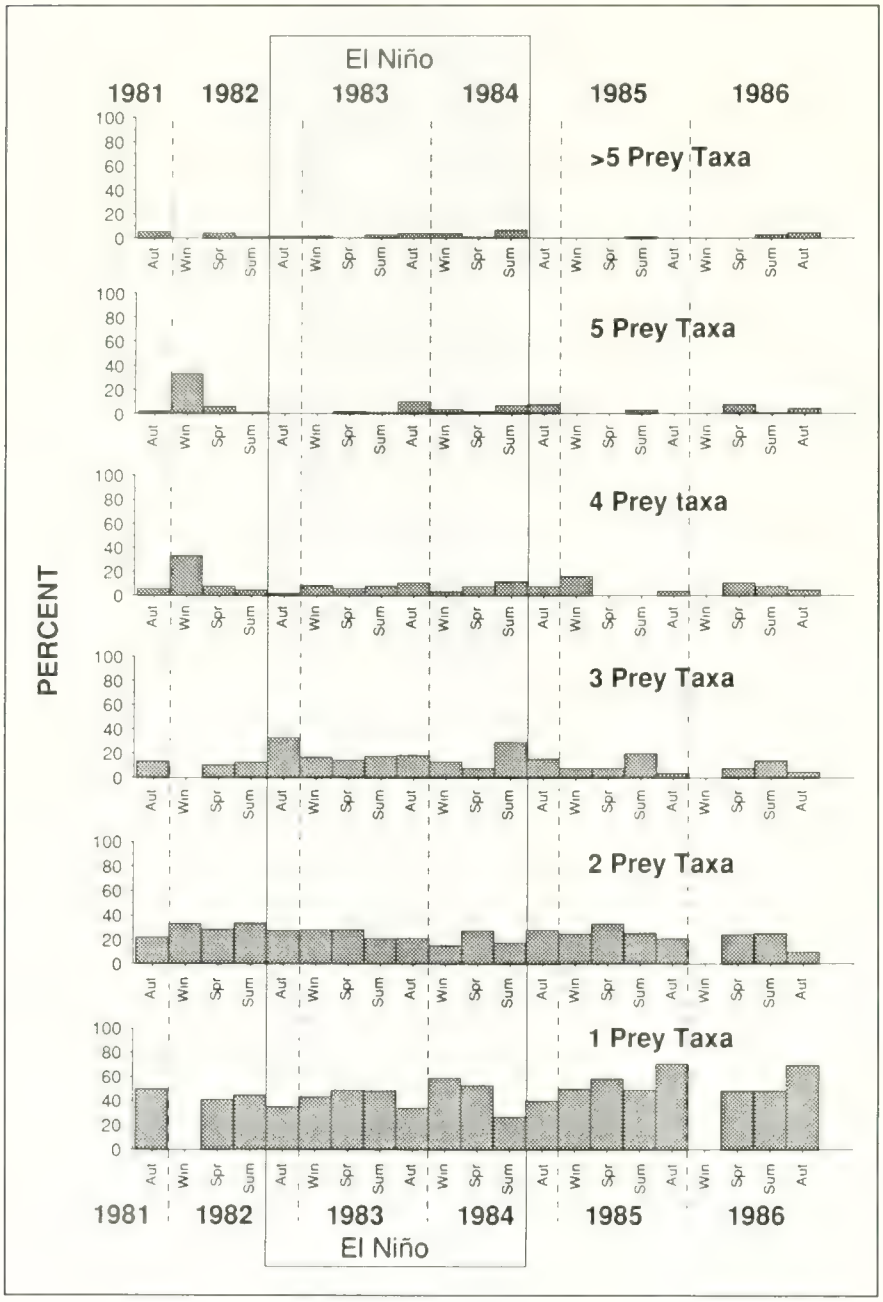


Figure 8
Seasonal occurrence of single and multiple prey taxa found in 1304 California sea lion scats, 1981–86. No samples were collected in winter 1986.

The relative frequencies of different prey taxa per scat varied among seasonal sampling periods during the study period (Fig. 8). Relative frequencies of prey taxa per scat for years 1982–85 were the same for all seasons in 1983 ($\chi^2 = 22.067$, df = 15, $P = 0.1061$) and 1985 ($\chi^2 = 18.219$, df = 15, $P = 0.2513$), but greater numbers of prey taxa were found in scats in 1982 ($\chi^2 = 35.892$, df = 15, $P = 0.0018$) and 1984 ($\chi^2 = 44.046$, df = 15, $P = 0.0001$).

Discussion

California sea lions using SCI consumed a variety of prey, consisting primarily of fish and cephalopods as indicated by the presence of fish remains in 98.5% of the scats and cephalopod remains in 35.5% of the scats. They fed on schooling fishes (e.g., northern anchovy, jack mackerel, Pacific mackerel, Pacific whiting, blacksmith, and rockfish), schooling cephalopods (e.g., market squid; Hurley 1978), and pelagic crustaceans that drift in large swarms (e.g., pelagic red crab; Boyd 1967). Our temporal analysis of nine prey taxa in-

dicated seasonal and yearly variability in the diet of SCI sea lions. Northern anchovy apparently was the major food source because it was represented by high index values and consistently occurred in the sea lions' diet during the 5-year period. Pelagic red crab, jack mackerel, Pacific whiting, rockfish, market squid, blacksmith, and Pacific mackerel appear to supplement the diet of California sea lions.

A major uncertainty with using scat analysis to study pinniped food habits is how these results reflect what was initially consumed by the animals. Studies on captive pinnipeds indicate that recovery rates are (1) lower than ingestion rates for all prey; (2) lower for prey species with small otoliths than prey with large otoliths; and (3) lower for young (i.e., small) prey than for older (i.e., large) prey of the same species (Hawes 1983, da Silva and Neilson 1985, Murie and Lavigne 1986, Dellinger and Trillmich 1988, Harvey 1989). Proportions of different prey species in scats were found to correspond to proportions of prey fed (Dellinger and Trillmich 1988). Pitcher (1980) found no difference between occurrence of fish in stomachs and feces of harbor seals *Phoca vitulina*, but cephalopods were under-represented in their feces.

The prey that occurred in 10% or more of scat samples ranged from small-sized (i.e., northern anchovy, market squid, and pelagic red crab) to prey that, when mature, could be potentially large-sized (i.e., Pacific whiting, jack mackerel, rockfish, and Pacific mackerel). Northern anchovy, being small-sized with small otoliths, would probably represent a higher proportion of the diet than indicated in scat samples. Market squid would also represent a higher proportion of the diet because beaks are often regurgitated and would be underrepresented in scats.

Results from SCI indicated differences in both prey composition and temporal variability from those described by Bailey and Ainley (1982) for sea lions at the Farallon Islands off central California. We found that several prey were consistently consumed (e.g., northern anchovy, jack mackerel, Pacific whiting, rockfish, market squid, blacksmith, and Pacific mackerel), whereas they reported only two prey (Pacific whiting and rockfish) that were regularly eaten. They found Pacific whiting to occur in the sea lions' diet during spring and summer, and juvenile rockfish during the fall and winter. At SCI we found that the presence of various types of prey in the diet of sea lions fluctuated year-to-year and sometimes seasonally within the same year. These differences between two island areas may be due to differences in the sampling periods (1981–86 for our study; 1974–78 for the Farallon Island study), to differences in prey availability in each area, or to differences in the sexual composition of animals inhabiting each area.

We would expect similar diets for sea lions using islands within close proximity of each other. Data from a study of food habits on San Miguel Island (SMI) during spring and summer in 1978–79 by Antonelis et al. (1984) were compared with our results. Four types of prey taxa (Pacific whiting, rockfish, northern anchovy, and market squid) were consistently found in scats of SCI and SMI sea lions. Jack mackerel, consistently found at SCI, was a minor prey item at SMI. The presence of pelagic red crab at SCI was due to the California El Niño, which did not occur during the SMI study. Blacksmith were not found in the diet of sea lions at San Miguel Island, but occurred frequently in the SCI study. Because the distribution and availability of these prey differ over time, we are unable to test our expected similarities in prey consumption until concurrent studies are conducted.

Availability and abundance of sea lion prey have been demonstrated by Bailey and Ainley (1982) and Antonelis et al. (1984) to influence diet of California sea lions. Evidence that abundance, if not availability, of prey influences consumption is also found from our study at SCI when we compare anchovy occurrence in scats with anchovy biomass estimates for each year (Bindman 1986, Methot and Lo 1987). The decline in the occurrence of anchovy in the scats during 1982 and 1984 coincided with lower estimates of anchovy biomass of 415,000 mt for 1982 and 309,000 mt for 1984 (Bindman 1986). Increased occurrence of anchovy in scats during 1983, 1985, and 1986 coincided with greater estimates of anchovy biomass: 623,000 and 522,000 mt (Bindman 1986), and 764,000 mt (Methot and Lo 1987), respectively. Decline in anchovy biomass may have caused SCI sea lions to consume other species in 1982 and 1984, resulting in increased occurrence in the latter.

There was more variability in occurrence of different prey taxa per scat in 1982 and 1984 when the estimated population biomass of anchovy was low, and less variability in 1983 and 1985 when there was a greater biomass. The diet of SCI sea lions, therefore, may be strongly affected by the abundance of northern anchovy. As anchovy becomes scarce, we expect SCI sea lions to consume other types of prey and exhibit greater variability in the number of different prey consumed.

We expected the non-El Niño periods to have similar occurrences of prey taxa consumed, which would differ from the El Niño distribution. In fact, all three periods exhibited significantly different distributions of prey taxa and in their occurrence.

The pattern in the commercial harvest of market squid (which is not affected by regulations and quotas) observed in California before, during, and after El Niño (Worcester 1987) closely resembled the pattern observed in the occurrence of this prey in the diet of SCI

sea lions. During the El Niño in 1983 and 1984 the commercial catch of market squid was 2010 and 622 short tons, respectively; prior to the El Niño it was 25,915 and 17,951 short tons for 1981 and 1982, respectively; and, after the El Niño it was 11,326 and 23,124 short tons for 1985 and 1986, respectively. The presence of market squid in the diet of sea lions during 1983 indicates the availability of this prey to sea lions, despite low availability to commercial catches. However, in 1984 when the commercial harvest was at its lowest, market squid was not detected in the sea lions' diet. Both the sea lions' consumption of market squid and the commercial catch were apparently affected by availability.

The effect of El Niño on the diet of SCI sea lions is also demonstrated by the presence of remains from pelagic red crabs in scat samples. Pelagic red crabs are normally found over the continental shelf of southern Baja California, and are sometimes transported into the SCB and further northward by the Davidson and California Countercurrents in January and February (Boyd 1967). These currents intensified as a result of the 1982–83 El Niño/Southern Oscillation, affected water temperatures in the SCB from late 1982 to October–November 1984, and carried pelagic red crabs from southern Baja California to the SCB where they were eaten by California sea lions.

The food consumed by the U.S. population of California sea lions could have an impact on the ecosystem and be in direct competition with commercial and sport fisheries. Six of the common prey of California sea lions identified at SCI (jack mackerel, northern anchovy, market squid, Pacific mackerel, Pacific whiting, and rockfish) are of value to commercial or sport fisheries. DeMaster (1983) estimated that California sea lions in U.S. waters (estimated population size 69,700) consumed roughly 115,000–295,000 mt of biomass per year. The present consumption would be greater than in 1983 because of the estimated 5% annual increase in the U.S. population (DeMaster et al. 1982). The growth in the sea lion population, and its estimated consumption, raises questions. Will there be greater competition between sea lions and fishermen for fish and squid as a result of increased numbers of sea lions? What will be the effect of population growth of sea lions on other elements of the SCB ecosystem?

Observed temporal differences in diet of sea lions from SCI during the California El Niño of 1982–84 clearly indicate the need for long-term studies of food habits of this predator throughout its range. Short-term studies may reflect oceanographic conditions of relatively short duration, such as El Niño, that strongly influence food supply and sea lion diet.

Acknowledgments

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Abstract.– Reproduction, age, growth, and mortality of the whitemouth croaker *Micropogonias furnieri* in Trinidad, West Indies, were studied. Maturity was attained at 2 years of age for both sexes. Spawning occurred year-round with a peak from February to August. The condition factor varied with the reproductive cycle. The sex ratio was 1:1.3 male:female. Fecundity ranged from 17×10^3 to 37×10^5 eggs for fish measuring 27.6–57.2 cm total length. Relationships between fecundity (F) and total length (TL) in centimeters, and body weight (W) and ovary weight (Wg) in grams, respectively, were: $F = 2\times10^{-4}TL^{5.56}$; $F = 0.81\ W^{1.88}$, and $F = 22525\,Wg - 81355$. The length-weight relationship was $W = 0.037TL^{2.64}$. Age was determined using otoliths and the analysis of length-frequency distributions. The von Bertalanffy growth equations were $L_t = 65.3\ \{1 - \exp\ [-0.16(t + 1.6)]\}$ for males and $L_t = 82.9\{1 - \exp\ [-0.13(t + 1.3)]\}$ for females. Total mortality rate was 1.2/year, natural mortality rate 0.4/year, and fishing mortality 0.8/year. Yield-per-recruit analysis showed the whitemouth croaker to be fully exploited in Trinidad.

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Reproduction, Age, and Growth of the Whitemouth Croaker *Micropogonias furnieri* (Desmarest 1823) in Trinidad Waters

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The whitemouth croaker *Micropogonias furnieri* (Desmarest 1823) is found in most of the Antilles, and along the southern Caribbean coast and Atlantic coast of South America from Costa Rica to Argentina (Fischer 1978). Important fishing grounds extend from Venezuela to Uruguay. This species is one of the most economically important demersal fish in Trinidad, where it is caught mainly by trawling and bottom longlines. Juvenile croakers also constitute a significant portion of the shrimp bycatch, most of which is discarded at sea.

Relevant studies have been conducted in Brazil and include general biology (Vazzoler 1962); age and growth (Rodrigues 1968); reproduction, population diversification, and growth (Vazzoler 1970, 1971); feeding habits (Tanji 1974); growth and sexual maturation of juveniles (Castello 1982); and reproductive biology (Isaac-Nahum and Vazzoler 1983).

Presented in this paper are some aspects of the biology, including reproduction, growth, mortality, and yield-per-recruit (Y/R) analysis, of the croaker in Trinidad waters.

Materials and methods

Study area

The island of Trinidad lies between lat. 10°2′N and 10°50′N and long. 60°54′ and 61°56′W on the South American Continental Shelf. Wide expanses of flat, muddy, relatively shallow substrate are found in the coastal areas where trawling for demersal fish and penaeid shrimps is carried out. The climate is tropical with a dry season from January to June and a wet season from July to December. Sampling was done in the northwestern waters of Trinidad in depths of 30–60 m.

Methods

Between October 1977 and September 1982, 2314 croakers were obtained by trawling. The vessels were of steel hull, 25–29 m in length, and carrying two side trawls. The opening of the trawl nets ranged from 13.7 to 18 m at the head end while the cod end mesh size was 2.5 cm. The catch was sorted into species and placed in separate baskets, each with a capacity of about 32 kg. Depending on the size of the catch, 2–3 baskets of croaker were taken at random for analysis. Total length (TL) in centimeters, body weight (W) and gonad weight (Wg) in grams, and sex and gonad maturity stage were recorded.

Four maturity stages were recognized macroscopically (following Vazzoler 1971): immature, maturing, mature (ripe), and spent. Mature ovaries were weighed to the nearest gram

and preserved in Gilson's fluid (Simpson 1951), and fecundity determined using a volumetric method (Bagenal and Braum 1971). Condition factor (CF) was determined from the formula $CF = 100\,W/TL^3$ (Hile 1936).

Age was determined using otoliths (sagittae) from a total of 252 fish. Longitudinal sections of otoliths were prepared following the technique described by Holden and Raitt (1974). Sections were wet with water and viewed against a black background using reflected light. Distinct alternating broad opaque and narrow translucent rings were present and the latter were assumed to be annuli. Rings were determined to be annual by using the marginal increment technique (e.g., Moe 1969, Turner et al. 1983). Otoliths were reread by the same worker one month after the initial reading and a 90% agreement was found, while a 92% agreement was found with another worker's readings. Marginal increment and otolith radius were measured using an ocular micrometer (1 micrometer unit = 0.05 mm).

Attempts were also made to determine age by analyzing the length-frequency distribution using cumulative probability paper. Total length was plotted against percentage cumulative frequency, resulting in a Cassie curve (Cassie 1954). Age groups were separated using points of inflexion which were chosen by eye. Only fish caught during March–May 1978 were used in this analysis.

The von Bertalanffy (1938) model was used to describe growth:

$$L_t = L_\infty \{1 - \exp[-K(t - t_0)]\}$$

where L_t is length at time t, K is the growth coefficient, L_∞ is the asymptotic length, and t_0 is the hypothetical age at zero length. These parameters were estimated utilizing the Length Based Fish Stock Assessment (LFSA) Package of BASIC computer programs (Sparre 1987).

Total annual mortality rate (Z) was estimated from a length-converted catch curve (Pauly 1984). Natural mortality rate (M) was determined from the empirical relationship derived by Pauly (1980):

$$\log M = 0.0066 - 0.279 \log L_\infty + 0.6543 \log K + 0.4634\ T,$$

where T is the mean water temperature which was 26.2°C in this area. Fishing mortality (F) was calculated as the difference between Z and M (Ricker 1975).

Yield per recruit (Y/R) in grams was determined from the model of Beverton and Holt (1957). Analyses were carried out using the LFSA package. The input parameters were W_∞ (determined from the formula $W = a\,L_\infty^b$), K, t_0, M, t_c (age at first capture of 2 years), which was determined by mesh selectivity experiments (Sylvester 1986), and t_r (age at recruitment). Examination of length-frequency distributions of catches indicated that croakers were fully recruited at a total length of 25 cm, or 1 year of age. The average values of K and t_0 for both sexes were used. Y/R analysis was done for a range of M values to determine their effects on conclusions drawn.

Table 1
Percentage of mature male and female croaker by size group in Trinidad waters.

Total length (cm)	Percentage mature	
	Male	Female
22–24	1	4
24–26	6	20
26–28	44	16
28–30	61	17
30–32	67	49
32–34	74	70
34–36	97	85
36–38	97	89
38–40	97	96
40–42	100	100
42–44	100	100
44–46	100	100
46–48	100	100
48–50	100	100
50–52	100	100
52–54	100	100
54–56		100
56–58	–	100

Results

Size at maturity

The percentage of mature males and females in each 3-cm size group is shown in Table 1. The size at which 50% of the fish examined were mature was about 28 cm for males and 32 cm for females.

Spawning pattern

Examination of the monthly frequency of croakers in each developmental stage showed the presence of all stages throughout the year (Table 2). A higher percentage of ripe fish was found from February to August, indicating an intensification of spawning during this time.

Sex ratio

The overall sex ratio of 852 croakers was 1:1.3, male: female. This was significantly different from 1:1 (P

Table 2
Monthly percentages of croaker by developmental stage in Trinidad waters.

Maturity stage	J	F	M	A	M	J	J	A	S	O	N	D
Immature	33	32	23	2	25	48	27	19	—	15	23	37
Maturing	11	34	48	27	40	42	40	32	—	52	58	59
Mature	17	32	20	27	24	10	18	27	—	10	4	3
Spent	39	2	9	44	11	0	15	22	—	23	15	1
N	18	47	141	59	63	42	337	81	—	134	116	80

<0.001). Monthly sex ratios showed a higher proportion of females from March to October and of males from November to February.

Fecundity

Fecundity estimates for 24 fish measuring 27.6–57.2 cm ranged from 17×10^3 to 37×10^5 eggs. Mean number of eggs per gram ovary-free body weight was 449 with a standard deviation of 169. Relationships between fecundity and total length, body weight, and ovary weight were described by the following respective regressions:

$$F = 2 \times 10^{-4}\mathrm{TL}^{5.56} \quad (r^2 = 0.90)$$

$$F = 0.81\mathrm{W}^{1.88} \quad (r^2 = 0.89)$$

$$F = 22525\mathrm{Wg} - 81355 \quad (r^2 = 0.99)$$

Length-weight relationship

The length-weight relationship for males was $\mathrm{W} = 0.035\mathrm{TL}^{2.66}$ and for females $\mathrm{W} = 0.030\mathrm{TL}^{2.69}$. Analysis of covariance showed no significant difference between the two sexes ($P>0.05$), therefore the data were pooled and one relationship established: $\mathrm{W} = 0.03\mathrm{TL}^{2.64}$. Asymptotic weight ($W_\infty$) was 3641.6 g.

Condition factor

Monthly variation in condition factor for males and females is shown in Figures 1 and 2, respectively. The condition factor was lowest in August for both sexes while it was highest in April for males and in May for females.

Age and growth

Mean marginal increments were lowest from May to August, indicating that annulus formation occurred during this period (Fig. 3). Fish length was directly proportional to, and highly correlated with, otolith radius (R): $\mathrm{TL} = 12.0 + 32.7\mathrm{R}$, ($r^2 = 0.94$). Otolith reading showed the presence of six age groups for males and seven for females, while analysis of length-frequency

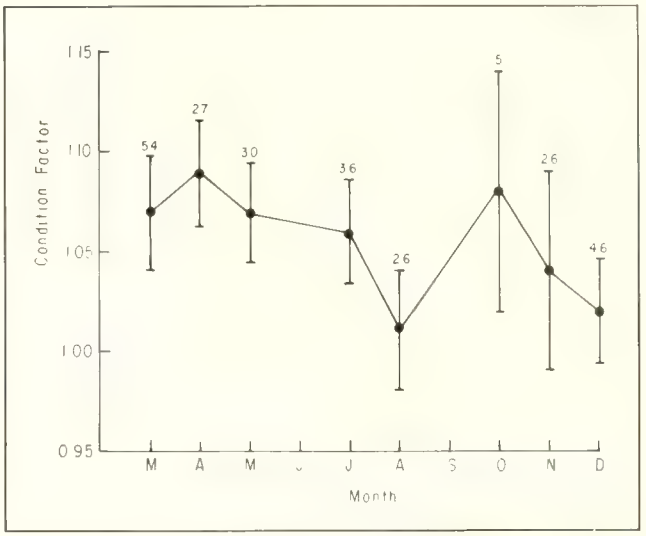

Figure 1
Mean monthly condition factor (±95% CL) of male croaker in Trinidad waters. Number of fish is given for each month.

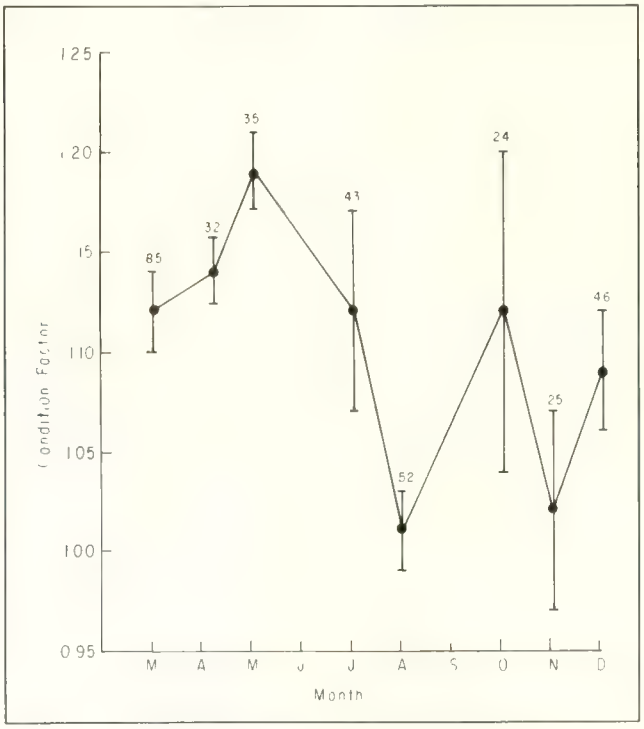

Figure 2
Mean monthly condition factor (±95% CL) of female croaker in Trinidad waters. Number of fish is given for each month.

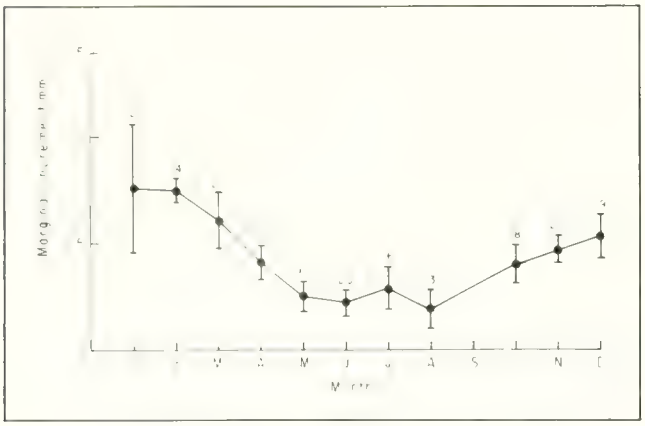

Figure 3
Mean monthly marginal increment (±95% CL) of otoliths of the croaker in Trinidad waters. Number of fish is given for each month.

distribution of combined sexes showed six age groups (Fig. 4). There was close correspondence in lengths at respective ages found by the two methods (Table 3). Based on the above, use of otoliths for age determination of the croaker is considered to be valid. A preliminary plot of the observed length at age revealed that growth of the croaker could be adequately described by the von Bertalanffy equation. Growth parameters showed that females achieved a greater asymptotic length, but grew at a slower rate than males. In Table 4 these parameters are compared with those found for different populations of croaker in Brazil.

Mortality

Total mortality rate (Z) which was the slope of the descending part of the length-converted catch curve in Figure 5 was 1.2/year ($r^2 = 0.96$, $P<0.05$). The 95% confidence limits for Z were 0.91 and 1.49. Natural mortality rate (M) was 0.4/year, and fishing mortality rate (F) was 0.8/year.

Yield per recruit

At the present level of F and t_c, Y/R is already at the maximum of 175 g (Fig. 6). Increasing F results in a decrease in Y/R. Increasing t_c to 3 years results in a Y/R of 181 g at the same level of F. At values of M of 0.1, 0.2, and 0.3 the croaker is overexploited at the corresponding levels of F (Fig. 7), while at M of 0.4 and 0.5 it is fully exploited. At low M values the yield curves are domed with peaks at low F values, while at higher M values they are relatively flat.

Discussion

Several similarities exist in the reproductive biology of the whitemouth croaker throughout its geographical range. Early maturity and year-round spawning have

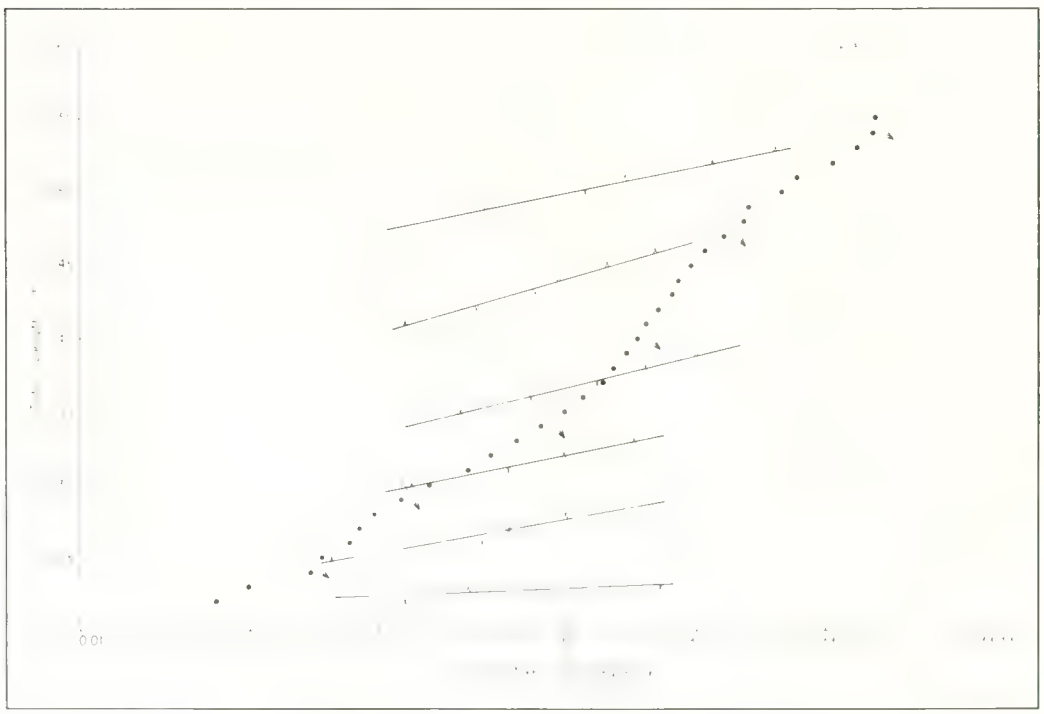

Figure 4
Cumulative percentage length frequency curve (dotted line) and separation into six age groups (straight lines) for the croaker in Trinidad waters. Arrows indicate inflexion points chosen by eye.

Table 3

Mean length at age determined from otolith sections and length-frequency distribution of the croaker in Trinidad waters.

Age group	Otoliths (TL ± SD) Male	*N*	Female	*N*	Length-frequency distribution (±SD)
I	22.0 ± 1.92	26	21.6 ± 2.09	23	22.3 ± 0.35
II	28.3 ± 1.85	21	29.4 ± 2.71	34	27.3 ± 1.65
III	33.6 ± 1.49	14	34.2 ± 1.89	18	31.6 ± 1.65
IV	38.5 ± 2.36	29	40.5 ± 1.98	30	36.2 ± 2.05
V	42.5 ± 1.83	10	47.5 ± 2.94	12	43.5 ± 2.45
VI	45.6 ± 2.79	10	51.6 ± 2.90	14	49.5 ± 1.70
VII	— —	—	53.5 ± 3.25	11	— —

Table 4

von Bertalanffy growth parameters of the croaker in Trinidad and Brazil waters.

Area	Sex	L_∞	K	t_0	Structure	Author
Brazil (33–29°S)	F	69.33	0.149	−2.79	scales	Vazzoler 1971
	M	89.57	0.076	−4.64		
Brazil (29–23°S)	F	60.10	0.219	−2.08	scales	Vazzoler 1971
	M	82.90	0.106	−2.97		
Brazil (4°S)	F	67.60	0.18	−0.42	scales	Rodrigues 1968
	M	68.60	0.18	−0.52		
Trinidad	F	82.90	0.13	−0.13	otoliths	This study
	M	65.30	0.16	−0.16		

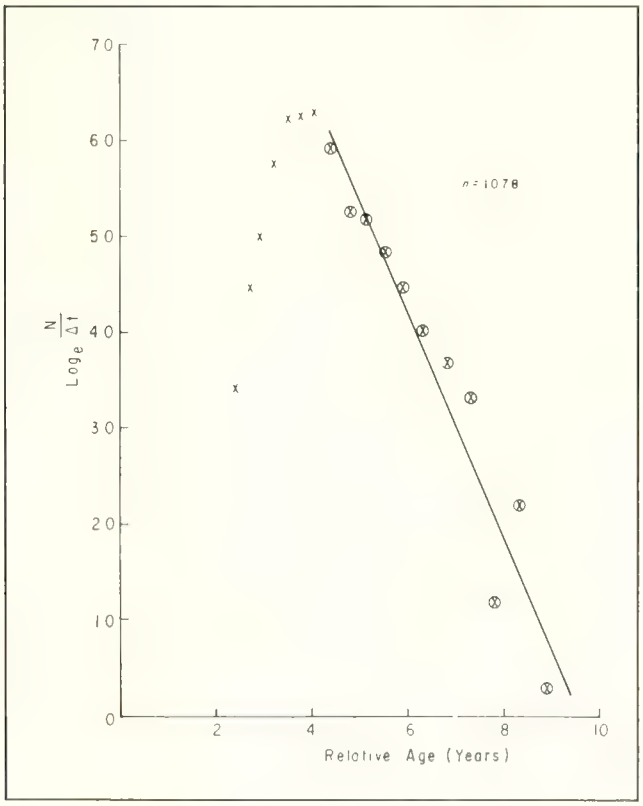

Figure 5

Length-converted catch curve of the croaker in Trinidad waters. (⊗) points used to find *Z*; (x) ascending part of curve, not used in analysis.

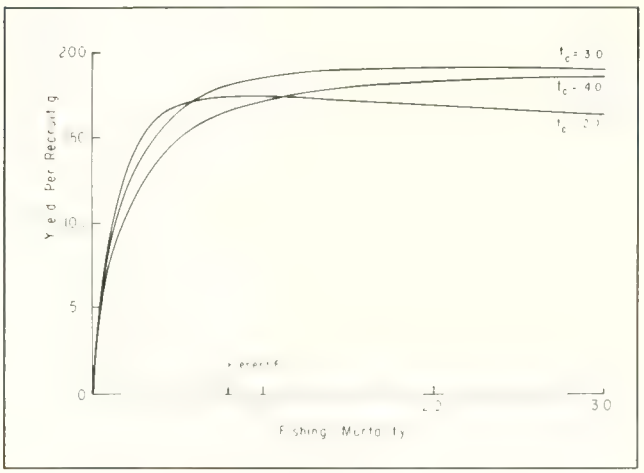

Figure 6

Yield per recruit (g) of croaker in Trinidad waters against fishing mortality for age at first capture of 2, 3, and 4 years.

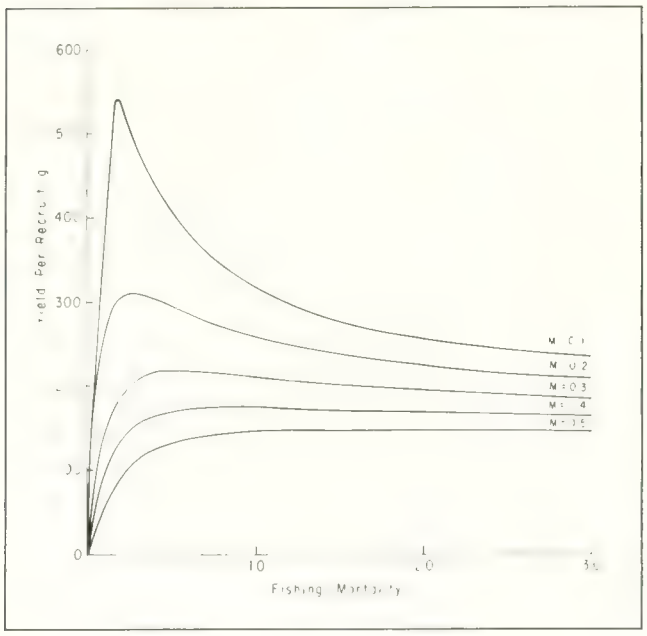

Figure 7

Yield per recruit (g) of croaker in Trinidad waters against fishing mortality for natural mortality rates of 0.1, 0.2, 0.3, 0.4, and 0.5 per year.

also been recorded in Brazil (Vazzoler 1962, 1971; Castello 1982; Isaac-Nahum and Vazzoler 1983), and in Guyana (Lowe-McConnell 1966).

Other workers have been successful in determining the age of tropical and subtropical sciaenids using otoliths (e.g., Bayagbona 1969, Villyamar 1972, Pannella 1974, Barger 1985). Annulus formation coincides with both the period of peak spawning and the wet season when salinity decreases due to river run-off. A similar pattern occurs in other species of tropical sciaenids (e.g., Rao 1966, Le Guen 1971). The annulus in immature croaker is probably formed in the wet season of the year following their year of birth. Use of the Cassie method had two disadvantags: the subjectivity in choosing the inflexion points and the crowding of older age groups into the upper part of the cumulative frequency curve. However, the close agreement of results obtained by both methods validates the use of otoliths for age determination of the croaker.

The higher value of K for males than for females suggests a higher mortality rate for the former (Beverton and Holt 1959). This could also account for the presence of only six age groups for males and the predominance of females in the population.

The variation in growth between Trinidad and Brazil indicates that the croaker does not present a uniform population in this region. According to Vazzoler (1971) geographical differences in growth characteristics of this species are due to genotypical and ecological factors such as salinity and temperature.

Estimation of mortality rates from length-converted catch curves is subject to several assumptions, the most important of which is that of constant recruitment (Ricker 1975). Examination of length-frequency distributions indicated that the modal length in the catch was similar for all years of sampling (33.0–34.9 cm), and no particularly strong or weak year class was apparent. Another assumption is that of constant fishing effort, which did not change appreciably during the period of sampling, as indicated by the number of active vessels. Since only fully recruited age groups were used in this analysis, Z was assumed to be constant over these ages. Trawling was considered to be a random method of sampling for older, fully recruited age groups, and the sample was assumed to be representative of that part of the population which was used to compute Z. Violation of these assumptions often results in non-linear right limbs of catch curves (Ricker 1975). However, the linear right limb of the catch curve in this study and the significant regression suggest that the estimate of Z is acceptable.

All of the conditions, except that of isometric growth, accompanying the Beverton and Holt model are assumed to exist for the croaker. The assumption of isometric growth, when growth is in fact allometric, leads to incorrect estimates of yield (Paulik and Gales 1964). However, the absolute levels of these estimates are not of as much interest as the differences in yield that result from varying t_c and/or F. The relative error in such differences, when using an incorrect b, tends to be much less than that in the absolute levels (Ricker 1975).

Locally, fishing is the major cause of mortality of the croaker. At the present t_c and the level of F the maximum sustainable Y/R is already being obtained, and any increase in F would result in overexploitation. Increasing t_c to 3 years may not be economically worthwhile since the resulting increase in Y/R is only 6 g. Such a move however, would protect 2-year-old fish that are spawning for the first time. Because of the flattening of the yield curves at high F values, the effect of overexploitation on yield is small. However, the effects of overexploitation on recruitment is unknown, and requires future study.

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Abstract.–Commercial and recreational catches of red drum *Sciaenops ocellatus* were sampled from Tampa Bay and Mosquito/upper Indian River Lagoon, Florida, between August 1981 and March 1983. Males matured at smaller sizes and younger ages than did females. Males matured when they were 350–799 mm FL (ages 1–3), and females matured when 550–899 mm (ages 3–6). In 1981 and 1982, red drum spawned between August and November, with peak spawning occurring in September–October. Histological evidence suggested that spawning occurred in nearshore Gulf of Mexico waters, in passes, and in the estuary. Ages determined from thin sections of otoliths were validated by length-frequency and marginal-increment analyses for fish ages 1–3 and by observations of oxytetracycline-marked fish for ages 5, 12, 16, and 18. Growth was rapid through age 4 or 5 but then slowed markedly. Growth rates of males and females were similar on each coast. Estimates for the von Bertalanffy growth equation parameters K and t_0 were not significantly different between coasts; however, L_∞ was significantly greater on the Atlantic coast. Therefore, predicted lengths of Atlantic fish were greater at all ages. Maximum observed lengths were 980 mm on the Gulf coast and 1110 mm on the Atlantic coast. Maximum observed ages of sampled fish were 24 years on the Gulf coast and 33 years on the Atlantic coast. The range of 95% confidence intervals for estimates of total annual mortality rate on the Gulf coast was 87–98% for ages 2–4; on the Atlantic coast, the range was 50–76% for ages 2–6.

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Reproduction, Growth, and Mortality of Red Drum *Sciaenops ocellatus* in Florida Waters

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The red drum *Sciaenops ocellatus* is an estuarine-dependent sciaenid found in nearshore waters (usually <22 m deep) from northern Mexico to Massachusetts (Yokel 1966, Lux and Mahoney 1969, Ross et al. 1983); it is occasionally found north of Chesapeake Bay (Yokel 1980). Red drum support important recreational and, until recently, commercial fisheries in most coastal areas of the U.S. south Atlantic and Gulf of Mexico (Mercer 1984). These fisheries have recently undergone strict management in Florida to reduce growth and recruitment overfishing (Swingle et al. 1984, Goodyear 1987).

Despite the importance of the red drum, little is known about its life history in Florida. While the spawning season and size at maturity have been described for red drum in Texas (Pearson 1929, Miles 1951, Matlock 1985) and Mississippi (Overstreet 1983), the spawning season in Florida has been inferred only from larval collections taken along the Gulf coast (Springer and Woodburn 1960, Yokel 1966, Jannke 1971, Peters and McMichael 1987). Age and growth have been described for juvenile and adult red drum in U.S. south Atlantic waters (Bearden 1967, Theiling and Loyacano 1976, Music and Pafford 1984, Daniel 1988) and in the northern and western Gulf of Mexico (Pearson 1929; Simmons and Breuer 1962; Rohr 1964, 1980; McKee 1980; Doerzbacher et al. 1988). In Florida, larval and juvenile age and growth have been studied in Tampa Bay (Peters and McMichael 1987), but only limited data are available on early growth in other areas (Kilby 1955, Roessler 1967).

This paper describes reproduction, age, growth, and mortality for red drum on the Gulf and Atlantic coasts of Florida. Weight-length and length-length relationships are also presented.

Methods and materials

From August 1981 through March 1983, monthly samples of red drum were collected from commercial and recreational catches in two coastal areas of Florida: (1) Tampa Bay (27° 40′N, 82°35′W) on the Gulf coast, and (2) Mosquito/upper Indian River Lagoon (28°40′N, 80°40′W) on the Atlantic coast. Fish were captured using a variety of gear, including trammel nets, gill nets, hook-and-line, and haul seines. Fork length (FL) in millimeters was measured on all fish in the catch. Each month on both coasts, a random subsample was taken, and up to ten fish per length interval (<300, 400–499, 500–699, 700–899, and >899 mm) were measured for total length (TL) and standard length (SL), weighed for whole weight (W) to the nearest ounce (later converted to grams), and sampled for gonads and otoliths (sagittae). Gonads were preserved in the field in Davidson's or Zenker's fixative (Humason 1972), soaked in water for 24 hours in the laboratory, and then stored in 70% ethanol. A

Table 1
Reproductive classes of red drum gonads of each sex.

Class	Female	Male
1. **Immature**	Few folds of ovigerous lamellae; few or no primary oocytes; oogonia predominate; diameter of ovary <3.0 mm.	Only spermatogonia present; no evidence of tubule development.
2. **Developing**	Ovigerous lamellae fill lumen of entire gonad; abundant primary oocytes; oogonia present at periphery of lamellae.	Early spermatogenesis; few scattered cysts of primary spermatocytes; peripheral tubules differentiating lumen not developed.
or		
Resting virgin	Lamellae contain abundant primary oocytes; few, if any, oogonia present; absence of atretic oocytes; tunica thickened.	
3. **Maturing**	Early vitellogenesis; oogonia, primary oocytes, and oocytes with yolk vesicle present.	Mid-spermatogenesis; spermatogonia, cysts of spermatocytes and a few spermatids present along tubules.
4. **Mature**	Late vitellogenesis; oogonia, primary oocytes, and oocytes with yolk vesicles and yolk globules present.	Late spermatogenesis; few spermatogonia; spermatozoa collecting in tubules and central lumen.
5. **Gravid**	Maturation. Oogonia, primary oocytes and oocytes with yolk vesicles, globules, and migrating nuclei present.	Reduced number of spermatogenic cysts; efferent ducts filled with spermatozoa; lumen of central duct partially filled with spermatozoa.
6. **Spawning**	Amorphous, hydrated oocytes present; oogonia, primary oocytes, and oocytes with yolk vesicles, yolk globules, and migrated nuclei present; fragments of ruptured oocytes scattered throughout; collapsed, empty follicles present; yolk remnants usually present in connective tissue and lamellae; tunica greatly thickened.	Efferent ducts filled with spermatozoa; spermatozoa in main collecting duct; distal portions of a few efferent tubules empty and somewhat thickened; spermatogonia absent.
or		
Partially spent		
7. **Spent**	Oogonia and primary oocytes present in budding ovigerous lamellae; ovary with "empty" areas; "plugs" of unshed oocytes present; atretic oocytes scattered throughout, usually in association with blood vessels.	No spermatogonia or spermatocytes present; efferent tubules empty; lumen of central collecting duct with few sperm; testis greatly reduced in size; tunic of previous spawners thickened and convoluted.
8. **Recovering**	Prolific recrudescence of ovigerous lamellae with myriad oogonia and primary oocytes; only gamma and delta atretic oocytes present in the lamellae. Tunica thickened and convoluted.	Network of efferent tubules lined with spermatogonia; numerous PAS leucocytes present in central sinus; tunica thickened and convoluted.

6-mm-thick sample from the central portion of one lobe of each gonad was embedded in paraffin, sectioned to 6-μm thickness, stained with Mayer's haematoxylin (Humason 1972) and eosin Y, and mounted for microscopic examination. Additionally, sections of vitellogenic ovaries fixed in Zenker's fluid were sectioned to 8-μm thickness and stained with Heidenhain's azan (Humason 1972).

Eight classes of maturity (Table 1) were distinguished based on the histological criteria of Wallace and Selman (1981) and Hunter and Macewicz (1985) for oogenesis and Grier (1981) and Grier et al. (1987) for spermatogenesis. Recognition of oocyte atresia and rejuvenation was important in determining whether a fish had previously spawned. Atretic oocytes were recognized by degeneration of the zona radiata, nuclear membrane, and yolk globules (Moe 1969, Wallace and Selman 1981, Hunter and Macewicz 1985). "Rejuvenation" is defined as the development of oocytes that were held in an advanced perinuclear stage of development since the previous spawning season. These clutches of oocytes in postspawn, recovering females exhibited a characteristic dual cytoplasmic banding (Yamamoto 1956, Howell 1983).

Length at maturity was determined by grouping fish by coast and sex into 50-mm intervals, determining the percentage that were mature ($\geq$ class 4) within each interval, and estimating the length at which 50% of the fish were mature by interpolating between interval midpoints. Oocyte diameters, measured with an ocular micrometer, were used to define the spawning season. Only oocytes whose nuclei were included in the cross section were measured, because these have been shown to represent true oocyte diameters (Foucher and

Beamish 1980). A total of 100 oocytes in a randomly chosen lamella were measured in each female gonad to calculate mean oocyte diameters within subsamples. To further delineate the spawning season and characterize variation in egg size, ten of the largest oocytes from each section were also measured (DeMartini and Fountain 1981), and their mean was plotted against the collection date.

Otoliths were excised from subsampled fish, cleaned, and stored dry in vials. Sagittae were sectioned in the laboratory using a Beuhler Isomet Low-Speed Saw with diamond wafering blades. A 0.5-mm-thick section, cut through the core of the right sagitta, was mounted on a microscope slide with Coverbond Mounting Media. Each section was examined for age marks using a dissecting scope (32×) with reflected light. All sections were independently read once by two individuals; then, when necessary, a common reading was conducted. Determining age by simply counting annuli was not always possible because annulus formation occurs about 2–6 months after the anniversary of the actual hatching date (see "Age Determination and Growth" section). To assign ages accurately, we assumed a biologically realistic hatching date of 1 October (see "Spawning Size, Age, Season, and Location" section; Matlock 1984), and ages were incremented on this date. Observations of otolith sections from oxytetracycline (OTC)-marked fish served to directly validate opaque bands as annuli. Oxytetracycline-injected fish (intramuscular injection of 25 mg/kg body wt.) were held in outdoor ponds ($n = 4$) for subsequent recapture and examination after they were free for more than 1 year. All four fish were recaptured after 19 months.

Red drum captured by all gear types were included in the growth analyses. The von Bertalanffy (1957) growth equation, $FL = L_\infty (1 - \exp[-K(t - t_0)])$, was fit to observed age-length data by using the NLIN procedure (Marquardt option) of SAS (Vaughan and Kanciruk 1982). Growth equation parameters are defined as follows: L_∞ = the average fork length (mm) that a fish would achieve if it were allowed to grow indefinitely in accordance with the model; K = Brody's growth constant; t_0 = the hypothetical age at which a fish would have zero length, and t = age in years (Ricker 1975). The weight-length relationship was described by linear regression of $\log_{10}$-transformed data. Analysis of covariance was used to test for differences between regressions.

Age-length keys were applied to length frequencies to separate age groups and develop sample abundance data used to estimate total annual mortality rate (A): $A = 1 - S$, where S is the annual survival rate. Age-length keys were developed for each season for combined samples captured by trammel net, hook-and-line, and haul-seine. Abundance of each age-group in the samples was then summed over all seasons during the study period. Total annual mortality rates were estimated from truncated age data that included all fully recruited age-groups with sample abundance of five or more fish. This procedure eliminated any bias inherent in the collection of large fish (Chapman and Robson 1960). Survival rates were calculated using the modified Heincke method (Seber 1973), Robson and Chapman (1961) estimates developed for truncated age data, and catch curves.

Results and discussion

Spawning size, age, season, and location

Males matured at smaller sizes (χ^2-test, $p < 0.05$) and younger ages than did females on both coasts. Some Gulf coast males were sexually mature after they reached 400 mm, and some on the Atlantic coast were mature after they reached 350 mm (Table 2). Interpolated lengths at 50% maturity were 529 mm and 511 mm, respectively. Most males were mature at age 1 or 2, and all were mature by age 3 (see "Age Determination and Growth" section). Some Gulf coast females were sexually mature after they reached 600 mm, and some on the Atlantic coast were mature after they reached 550 mm. Lengths at 50% maturity were 825 and 900 mm, respectively. Some females were mature at age 3, and all were mature by age 6.

While results of previous investigations suggest that the size and age at which red drum mature may vary over its geographical range (Pearson 1929, Gunter 1950, Miles 1951, Overstreet 1983, Music and Pafford 1984), we show that there are also large maturational differences between sexes. Lengths at 50% maturity were about 300–390 mm smaller for males than females. In Mississippi, males and females began developing when they were 300–549 mm SL (358–629 mm FL); however, only after growing to 700 mm SL (792 mm FL) were more than 50% of the samples of either sex mature (Overstreet 1983). Female red drum in Texas matured during their fourth or fifth year, at about 750–850 mm TL (711–803 mm FL) (Pearson 1929, Miles 1951, Matlock 1985). A 755-mm TL (716 mm FL) male red drum sampled in Georgia had well-developed gonads and was apparently mature (Music and Pafford 1984).

Spawning peaked on both coasts of Florida from about September through October. Maximum oocyte diameters and the presence of eggs with yolk vesicles, globules, and migrating nuclei indicated that active

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 2

Percent of sampled red drum in each 50 mm FL length interval that were mature (≥ class 4) on the Gulf and Atlantic coasts of Florida. Numbers in parentheses are numbers of fish examined.

Fork length (mm)	Gulf		Atlantic	
	Male	Female	Male	Female
200–249		0 (3)		
250–299	0 (7)	0 (4)	0(10)	0 (7)
300–349	0(21)	0(17)	0 (7)	0(17)
350–399	0(18)	0(24)	9(22)	0(22)
400–449	16(19)	0(16)	16(19)	0(32)
450–499	24(21)	0(24)	35(20)	0(28)
500–549	47(19)	0 (6)	56(25)	0(18)
550–599	81(27)	0(24)	70(20)	7(15)
600–649	88(43)	2(53)	85(20)	0(26)
650–699	85(36)	4(28)	82(38)	0(18)
700–749	100(36)	28(36)	93(27)	0(36)
750–799	100 (6)	36(14)	94(17)	7(14)
800–849	100 (3)	50 (2)	100 (6)	7(14)
850–899	100 (1)	100 (3)	100 (4)	0 (1)
900–949	100 (6)	100 (3)	100 (1)	100 (1)
950–999	100 (2)	100 (2)	100 (2)	100 (9)
1000–1049		100 (1)	100 (1)	100 (5)
1050–1099			100 (2)	
1100–1149				100 (1)

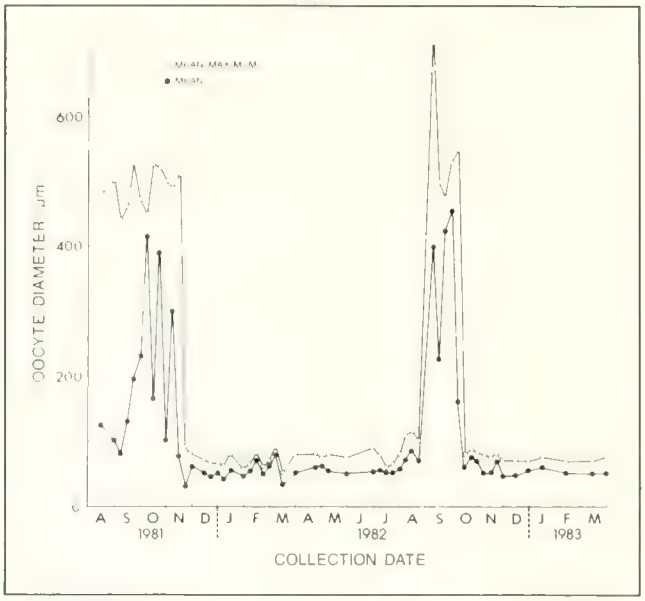

Figure 1

Mean and mean maximum oocyte diameters for red drum sampled from both Atlantic and Gulf coasts of Florida.

vitellogenesis occurred in August and September 1981, when the study began on the Gulf and Atlantic coasts, respectively (Fig. 1). Gonads were in spawning condition or were partially spent during September–October 1981. In 1982, active vitellogenesis began in August, and most spawning or partially spent individuals were collected in September. Mean and maximum oocyte diameters declined by mid-November 1981 and by mid-October 1982, indicating cessation of peak spawning (Fig. 1).

These results are consistent with the findings of previous studies (Pearson 1929, Mansueti 1960, Yokel 1966, Jannke 1971, Sabins 1973, Peters and McMichael 1987). However, spawning in Tampa Bay may have begun earlier than August in 1982 because larval and juvenile length-frequency distributions and otolith analyses of daily growth indicated that spawning had begun in mid-July (Peters and McMichael 1987). Apparently, spawning in mid-July did not occur in a large enough portion of the population to be reflected in our samples. Macroscopic analyses of adult gonads and analyses of gonosomatic indices have suggested that spawning takes place in Texas during October through February (Heffernan 1977) and that spawning off Mississippi takes place during summer (Overstreet 1983).

Ovarian histological features provided evidence that spawning occurs in the nearshore Gulf of Mexico, in the vicinity of passes, and within estuaries. Ovaries of females captured in all three areas displayed either (1) advanced oocytes with migrating nuclei or hyaline oocytes released from the follicular layer, indicative of an imminent spawn (DeMartini and Fountain 1981), or (2) atretic bodies and postovulatory follicles (POF), indicative of a recent spawn (Yamamoto and Yoshioka 1964, Takita et al. 1983, Hunter and Macewicz 1985). A female captured 4.8 km off the Florida Gulf coast had numerous oocytes with migrating nuclei, and a male from the same site had spermatozoa filling the efferent duct of the testes, both of which suggest imminent offshore spawning. A large female red drum captured about 7 km within the mouth of Tampa Bay contained ovulated hydrated oocytes, POF, and several atretic oocytes. All of these artifacts indicate that she had recently spawned. Supporting the hypothesis that estuaries are also used as spawning sites is the fact that females ($n = 4$) that had POF or hyaline oocytes released from the follicle layer were found about 42 km within Tampa Bay, 35 km south of Ponce de Leon Inlet in Mosquito Lagoon, and 90 km north of Sebastian Inlet.

Based on data from egg and larval collections made just inside passes, most investigators have concluded that red drum spawn principally in nearshore areas close to channels and passes (Pearson 1929, Miles 1950,

Simmons and Breuer 1962, Yokel 1966, Jannke 1971, Holt et al. 1985). Our data suggest that spawning may also occur over the nearshore continental shelf and in estuaries. Collections of mature or recently spent fish made in nearshore Gulf waters from just outside the barrier islands to depths of 69.5 m suggest that spawning takes place offshore in the Gulf of Mexico (Christmas and Waller 1973; Heffernan 1977; W.A. Fable, NMFS Panama City Lab., Drum seine observers trip report, 18–21 Aug. 1982. Memo 00.Sep.82*002148 to A.C. Jones, NMFS Miami Lab., 4 p.). Peters and McMichael (1987) reported that although most spawning in Tampa Bay occurred close to its mouth, some spawning probably took place in nearshore Gulf waters. Recent egg collections provide evidence that red drum spawn within Mosquito Lagoon (Johnson and Funicelli In press). Our collection of females in Mosquito Lagoon containing POF corroborate these findings and suggest that red drum found equally far within Tampa Bay may also be spawning within the estuary. Moreover, red drum movement was observed during a sonic tracking study in Mosquito Lagoon (Carr and Smith 1977, Carr and Chaney 1976) and little directed movement during the spawning season was noted.

Age determination and growth

Ages of red drum from 0 to at least 18 could accurately be determined using otoliths. Red drum sagittae showed clearly delineated, easily interpreted (100% agreement between counts) hyaline and opaque bands. Otoliths with 0–33 opaque bands were examined; they were taken from 1085 red drum (551 Gulf coast and 534 Atlantic coast) with size ranges of 225–1110 mm. Although ages of red drum were validated for only the first 18 years, we assumed, for age and growth analysis, that each opaque band represents an annual mark (annulus).

Minimally overlapping monthly length frequencies, a consistent marginal increment minima each year, and observations of oxytetracycline-injected fish supported the hypothesis that the opaque bands are annuli. Modal length progressions representing the 1978, 1979, 1980, and 1981 year-classes on the Gulf coast and 1980 and 1981 year-classes on the Atlantic coast could be followed in length frequencies (Figs. 2, 3). These length modes could be followed for fish up to 3 years-old and consistently agreed with lengths of fish having corresponding otolith-determined ages. The periodicity of the mean monthly marginal increment minima each winter (December–March) for fish having one or two opaque bands further suggests that opaque bands were deposited annually (Fig. 4). Opaque bands on fish older than age 3 are also probably annuli. Four adult red drum that were injected and held in outdoor ponds for 19 months deposited one opaque band each between release (August 1986) and recapture (March 1988). These fish were 5, 12, 16, and 18 years-old when recaptured.

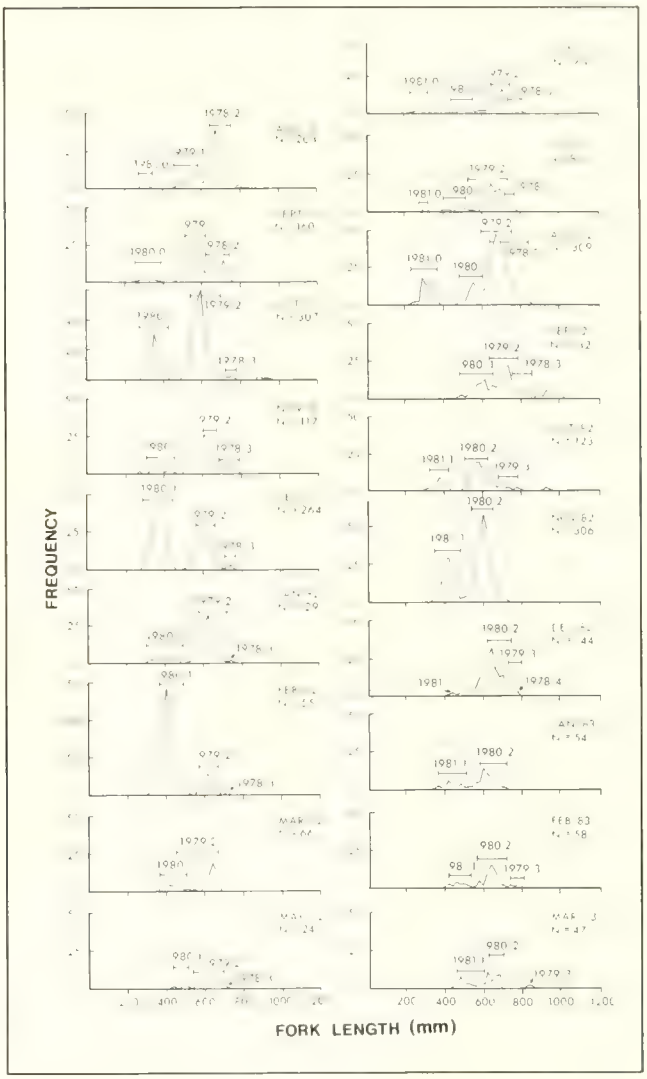

Figure 2

Monthly length frequencies for red drum from the Gulf coast of Florida. No collections were made in April 1982. Horizontal bars show length ranges for otolith-aged year-classes and are labeled for year-class and age in years.

Otoliths have been used to determine the age of red drum (Miles 1951, Rohr 1964, Theiling and Loyacano 1976), but the use of opaque bands as an age determinant has never been adequately tested. Off Mississippi, annuli apparently form on otoliths during winter or spring (Rohr 1964). In Texas, where the validity of using scales to determine ages of red drum ≤ 4.5 years-old has been established (Matlock et al. 1987), annuli form on scales between February and April in

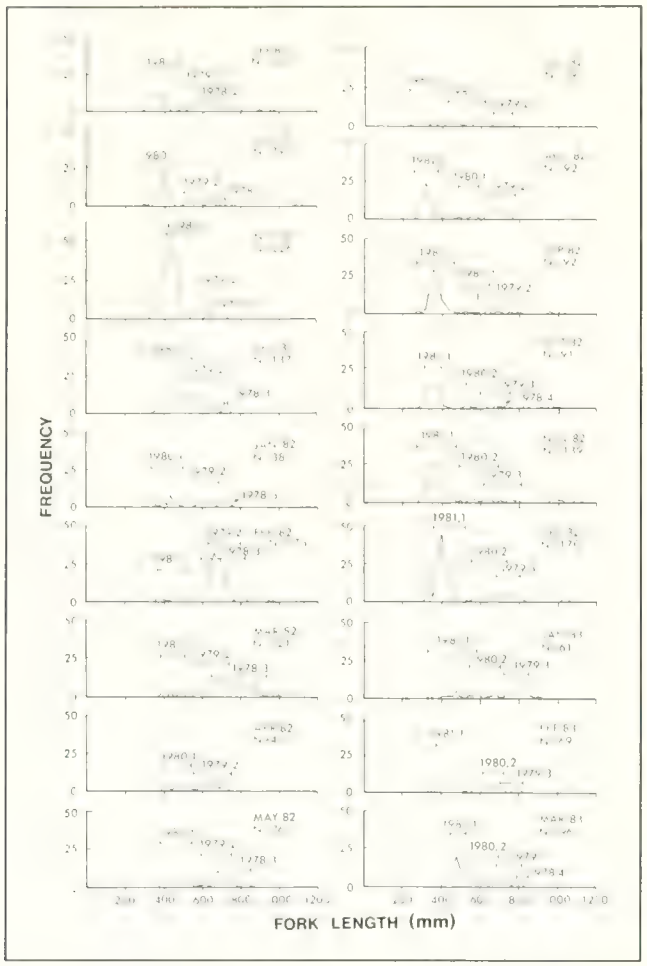

Figure 3

Monthly length frequencies for red drum from the Atlantic coast of Florida. No collections were made in June 1982. Horizontal bars show length ranges for otolith-aged year-classes and are labeled for year-class and age in years.

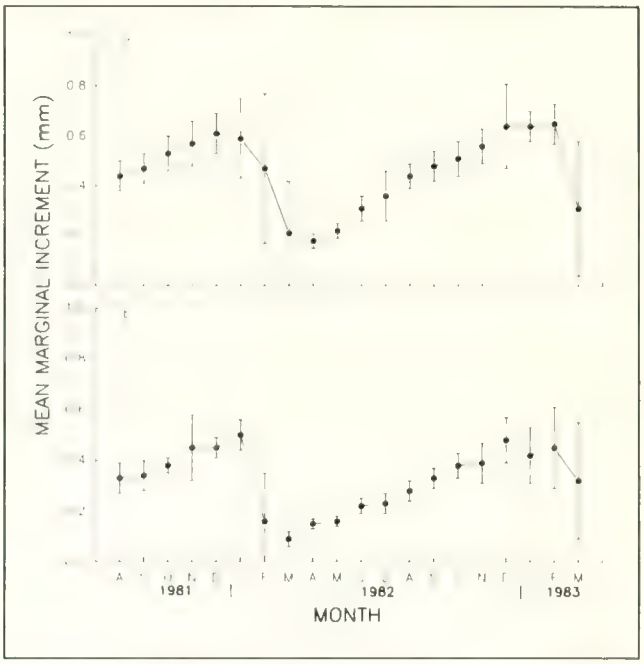

Figure 4

Mean monthly marginal increment (± 1 SD) for red drum in Florida waters with (a) one and (b) two annuli on otolith sections. Differences between coasts were not significant (ANOVA, $p>0.05$), therefore pooled data are presented.

Matagorda Bay (Wakefield and Colura 1983), during winter in Aransas/Corpus Christi Bay (Pearson 1929), and as early as January in all Texas bays (Matlock et al. 1987). Red drum deposit a first annulus on otoliths and scales during their second winter, when they are about 14–18 months-old (Pearson 1929, Rohr 1964, Theiling and Loyacano 1976, Hysmith et al. 1983, Wakefield and Colura 1983, Matlock 1984, Matlock et al. 1987). Apparently, juvenile red drum that measure 40–100 mm during their first winter (Kilby 1955, Peters and McMichael 1987) do not form an annulus; our smallest specimen with an annulus was 379 mm.

Red drum grew rapidly until age 4 or 5, and then growth slowed markedly (Table 3; Fig. 5). For each coast, the average observed sizes of fish ages 1–3 were not significantly different between sexes (Student's t-test; $p>0.10$ in all cases). However, in comparing coasts, the average observed sizes were significantly larger ($p<0.001$) at ages 1 and 2 on the Atlantic coast than they were on the Gulf coast. After age 2, growth appeared to be slower on the Atlantic coast; however, the variance for age 3 lengths was significantly greater (F-test; $p<0.05$) on the Atlantic coast. Sample sizes of older age groups were too small to test for statistical differences.

Lengths predicted from the von Bertalanffy growth curve agreed with the average observed lengths of red drum on the Gulf and Atlantic coasts (Table 3; Fig. 5). Asymptotic length (L_∞) was significantly larger (Student's t-test, $p<0.01$) on the Atlantic coast than on the Gulf coast, while the Brody's growth constant (K) and age at zero length (t_0) were not significantly different ($p>0.05$). Therefore, predicted lengths were greater at all ages for Atlantic coast red drum than for Gulf coast fish. Our estimates of asymptotic length are generally greater than other reported values: 717 mm TL (680 mm FL), 835 mm TL (789 mm FL), and 803 mm TL (760 mm FL) for Lower Laguna Madre, Matagorda, and Galveston Bays in Texas, respectively (Wakefield and Colura 1983); 918 mm TL (865 mm FL) in Texas bays (Doerzbacher et al. 1988); and 950 mm TL (894 mm FL) in Mississippi Sound (Rohr 1980). This suggests that red drum grow larger in Florida or, as

Table 3

Average observed and predicted fork lengths (mm) for red drum sampled from Gulf and Atlantic coasts of Florida. Sample sizes are in parentheses.

	Gulf		Atlantic	
Age (yr)	Average observed	Predicted	Average observed	Predicted
0	296 (62)		335 (59)	
1	436(169)	337	462(192)	373
2	635(232)	557	655(166)	581
3	736 (65)	696	742 (66)	718
4	845 (5)	784	768 (14)	808
5	877 (1)	839	863 (5)	867
6		874	871 (5)	905
7		896		931
8		910	995 (2)	948
9	975 (1)	919	973 (2)	959
10		925	986 (1)	966
11		928	918 (1)	971
12	925 (1)	930	894 (1)	974
13		932		976
14		933	1028 (2)	977
15		933	954 (1)	978
16		933	960 (1)	979
17	968 (1)	934		979
18	898 (2)	934		979
19	957 (1)	934	975 (1)	979
20		934		980
21	918 (1)	934		980
22	960 (6)	934	1110 (1)	980
23		934		980
24	980 (1)	934		980
25			1038 (3)	980
26			1060 (1)	980
27				980
28			983 (2)	980
29				980
30				980
31				980
32				980
33			1050 (1)	980

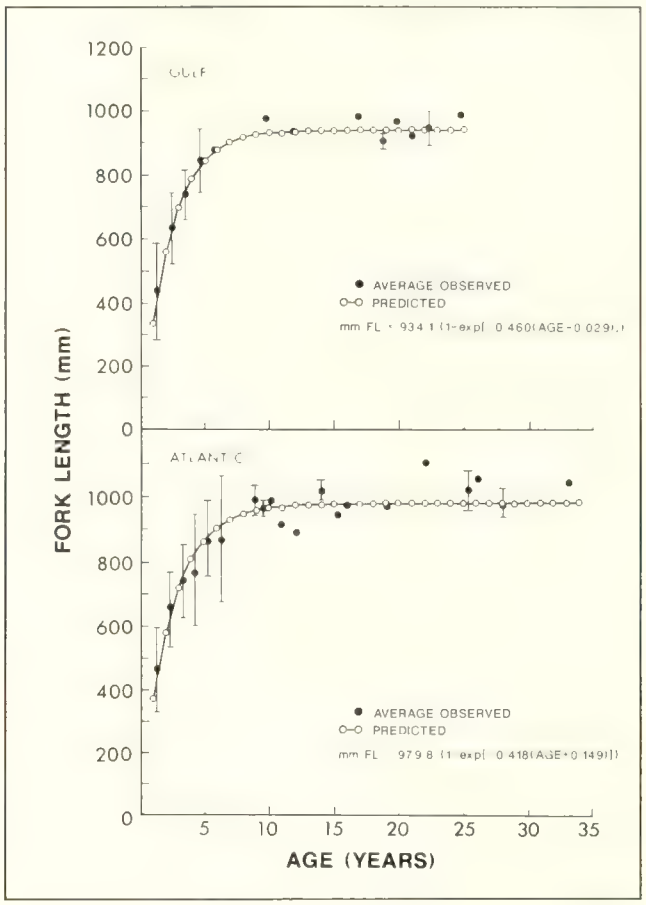

Figure 5

Average observed (±2 SD or range if $n = 2$; see Table 3) and predicted mean lengths of red drum in Florida waters.

noted by Matlock (1984), that the larger fish which predominately inhabit continental shelf waters were not adequately sampled in Texas and Mississippi. Matlock (1984) estimated the von Bertalanffy growth equation for red drum in Texas using data from Pearson (1929) and found what he considered a more reasonable estimate of L_∞ of 1068 mm TL (1002 mm FL).

Length-at-age estimates of red drum in Florida were similar to those reported in past literature for red drum in Texas (Pearson 1929, Miles 1951, Simmons and Breuer 1962; Table 4). However, red drum in Florida appear to grow more rapidly than red drum in Mississippi (Rohr 1980), South Carolina (Thieling and Loyacano 1976), and those in a more recent study from Texas (Wakefield and Colura 1983). However, as noted above the differences in length-at-age estimates could be attributed to a sampling bias toward smaller nearshore fish.

Mortality

Ninety-five percent confidence limits for estimates of total annual mortality rate (1 – S) using sample abundance data ranged 87–98% for red drum ages 2–4 on the Gulf coast and 50–76% for red drum between ages 2–6 on the Atlantic coast during 1981–83. Red drum were fully recruited by age 2. Sample size of fish older than 4 years on the Gulf coast and 6 years on the Atlantic coast fell below the suggested lower limit of five fish to ensure unbiased estimates (Chapman and Robson 1960). Mean estimates of total annual mortality rates were consistently greater for Gulf coast fish (Table 5).

Total annual mortality of red drum has been estimated for Everglades National Park in Florida and for Texas bay systems. In Everglades National Park, Rago

Table 4

Literature accounts of mean fork lengths at age for red drum. Fork lengths are in millimeters and were converted from TL or SL, if necessary, using the relationships in text.

	Age (yr)									
Area, study, and method	1	2	3	4	5	6	7	8	9	10
Texas										
Pearson (1929)										
Aransas/Corpus Christi Bays; length frequency	300	530	630	750	840					
Miles (1951)										
Aransas Bay; otoliths	380–423	575	630–684			826	871*	917–940		
Simmons and Breuer (1962)										
Lower coast; tag recapture	322	519	693							
Wakefield and Colura (1983)										
Lower Laguna Madre; scales	290	447	542							
Matagorda Bay; scales	255	399	526	605	660					
Galveston Bay; scales	275	439	547	619						
South Carolina										
Theiling and Loyacano (1976)										
otolith sections**	429	560	695	782	803	842	803			
Mississippi										
Rohr (1980)										
otoliths	356	522	638	717	772	810	839	853	867	875
Florida										
Present study										
Gulf coast; otolith sections	337	557	696	784	839	874	896	910	919	925
Atlantic coast; otolith sections	373	581	718	808	867	905	931	948	959	966

*A mixture of fish age seven and eight.
**Average size for age group from June through November.

Table 5

Pooled mean estimates and 95% confidence intervals of total annual mortality (A) for red drum ages 2–4 on the Gulf coast and ages 2–6 on the Atlantic coast.

	Total annual mortality			
	Gulf		Atlantic	
Method	A	95% CI	A	95% CI
Seber (1973)	0.92	0.91–0.94	0.65	0.59–0.70
Robson and Chapman (1961)	0.91	0.90–0.93	0.66	0.63–0.70
Catch curve	0.94	0.87–0.98	0.65	0.50–0.76

and Goodyear (1985) used tag-recapture days-at-large data to estimate a total annual mortality rate of 0.73 during 1984–85. Also based on tag-recapture data, total annual mortality rates in Texas bays were about 68% during 1976–77 (Matlock and Weaver 1979) and 80–87% during 1975–1979 (Green et al. 1985). Matlock (1984) estimated the total annual mortality rate to be 80% for all Texas bays during 1977–1981.

Apparent total annual mortality rates in Florida for red drum ages 2–6 are high, especially for a species that may live about 25–35 years. Theoretically, fish with such longevity (assuming constant mortality rate) would have a natural mortality rate of only about 12–18%; this rate allows for survival to the observed maximum ages (Royce 1972, Hoenig 1983). Our much greater estimates of total annual mortality for fish ages 2–6 may reflect one or more of the following: (1) a higher rate of natural mortality for younger fish (i.e., natural mortality is not constant), (2) high fishing-mortality rates within estuaries, and/or (3) emigration from estuaries (sampling area) before age 4 on the Gulf coast or age 6 on the Atlantic coast. In the first two cases, estimates of total mortality are unbiased, although component parts (fishing and natural mortality) are not the same. In the third case, total annual mortality would be overestimated because older fish that left the sampling area would be underrepresented in the catch.

While data for evaluating whether natural mortality changes with age are not available, tag-recapture data suggest that fishing mortality is high and that emigration does occur. Annual tag-return rates of

Table 6

Weight-length regressions of red drum sampled from the Gulf and Atlantic coasts of Florida. W = weight (g); FL = fork length (mm).

Area	N	FL (mm)	a (1 SE)	b (1 SE)	r^2
Gulf	491	242–1000	6.1673×10^{-6} (0.4301×10^{-6})	3.0984 (0.0114)	0.993
Atlantic	484	257–1110	9.3993×10^{-6} (0.6616×10^{-6})	3.0275 (0.0115)	0.993

Table 7

Length-length regressions of red drum in Florida. TL = total length (mm); FL = fork length (mm); SL = standard length (mm). Sample fork length range for all regressions was 225–1110 mm.

			$Y = a + bX$		
Y	X	N	a (1 SE)	b (1 SE)	r^2
FL	TL	1074	23.9383 (0.6704)	0.9162 (0.0011)	0.999
TL	FL	1074	−25.2080 (0.7600)	1.0898 (0.0013)	0.999
TL	SL	1075	10.3832 (0.8970)	1.1829 (0.0017)	0.998
SL	TL	1075	−7.6225 (0.7689)	0.8343 (0.0012)	0.998
FL	SL	1075	32.8951 (0.6934)	1.0850 (0.0013)	0.998
SL	FL	1075	−29.4619 (0.6738)	0.9202 (0.0011)	0.998

70–80% occurred in southwest Florida during the 1961–65 Schlitz Tagging Programs, and the average tag-return rate throughout the state was 46% (Beaumariage 1969). More recent annual tag-return rates in Florida were 11–25% (Murphy and Taylor 1985) and 12% (Rago and Goodyear 1985), but if these are adjusted to account for a probable low tag-reporting rate, e.g., 36% in Texas (Green et al. 1983), then actual annual recapture rates in Florida could still be high: 31–69%. Limited data on the emigration of red drum suggest a little exchange from estuarine to nearshore waters. Subadult red drum tagging studies within Tampa Bay have shown that about 2–6% of recaptured red drum came from outside the Bay (Murphy and Taylor 1985); similar results (1.4%) were reported for the Texas coast (Osburn et al. 1982). Fishing effort and "catchability" of red drum are probably lower in nearshore waters than within the estuary, which could cause the rates of emigration to be underestimated.

Weight-length and length-length relations

Weight-length regressions (Table 6) were not significantly different ($p>0.05$) between sexes on each coast,

Atlantic		
slope	df = 1, 480	F = 0.21
elevation	df = 1, 481	F = 0.34
Gulf		
slope	df = 1, 487	F = 1.60
elevation	df = 1, 488	F = 1.32,

although the slopes and elevations were different between coasts with sexes combined,

slope	df = 1, 971	F = 18.96
elevation	df = 1, 972	F = 27.5.

Predicted weights for subadult red drum were similar; e.g., the predicted weight of a 500-mm fish is about 1.4 kg on both coasts. However, adult red drum on the Gulf coast were heavier at a given length than they were on the Atlantic coast; e.g., a 900-mm fish weighs 8.8 kg on the Gulf coast and 8.3 kg on the Atlantic coast.

Length-length regressions show that total length and standard length increase more rapidly than fork length as fish get larger (Table 7). Total length is about 1% greater at 300 mm FL and 6% greater at 1000 mm FL. Standard length is 18% less than fork length at 300 mm FL but only 12% less at 1000 mm FL.

Summary

The following are significant features of the life history of red drum in Florida: rapid growth through age 4 or 5, relatively early sexual maturation (total maturity by age 3–6), a discrete peak in spawning activity during September–October, a life span of up to about 35 years, and spawning grounds located in nearshore waters, in passes and inlets, and inside large estuaries. These characteristics and the apparently high rate of annual mortality for red drum ages 2–6 suggest that only a small portion of the population survives to reach maturity. However, this annual rate of mortality (disappearance) has a component of emigration that warrants investigation. Recent management measures enacted by the Gulf of Mexico Fishery Management Council and the Florida Marine Fisheries Commission have limited fishing on the spawning stocks and have reduced fishing pressure on the immature fish.

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Abstract.– The sandfish family Trichodontidae is comprised of two species endemic to the boreal Pacific: *Arctoscopus japonicus* is a common demersal fish of commercial importance in the western area around northern Japan, while *Trichodon trichodon* is found in the eastern waters, from Alaska to California, although there is no fishery for this species. The two species share many similar reproductive features such as large demersal eggs of 3.3–3.5 mm diameter, moderate fecundities of 1000–2000 eggs, and peculiar spawning habits on rocky shores. However, there are striking contrasts in several reproductive and early-life-history traits: the shape of the egg mass is spherical in *A. japonicus* versus an irregular shape in *T. trichodon*; spawning substrate is mostly *Sargassum* spp. versus rock; incubation period is about 2 months versus nearly 1 year; and, at hatching, *T. trichodon* has precocious pectoral and caudal rays as well as preopercular spines. Despite these differences, larvae of both species appear in the spring season. These features are discussed in relation to the contrasting thermal regimes of the surface waters characteristic of each species. It is suggested that *A. japonicus* has a more derived reproductive style than *T. trichodon*, including a typical pattern of indirect ontogeny. The remarkable seasonal thermal events in Japanese coastal waters may be responsible for the notable abundance of *A. japonicus*.

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Contrast in Reproductive Style Between Two Species of Sandfishes (Family Trichodontidae)

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The family Trichodontidae is a small family of marine fishes endemic to the boreal Pacific comprised of two species, *Arctoscopus japonicus* (Steindachner) from the western Pacific around Japan and *Trichodon trichodon* (Tilesius) from the eastern Pacific, ranging from Alaska to California. As indicated by the common name "sandfishes," they typically lie partly buried in the bottom (Nelson 1984). Due to peculiar morphological and ecological features, they have been placed at various times in different groups of fishes such as the Percoidei (Matsubara 1963) and Blennioidei (Greenwood et al. 1966).

The biology of *A. japonicus* has been extensively studied because of its special importance to commercial fisheries in northern Japan and Korea (for review, see Ochiai and Tanaka 1986). For *T. trichodon*, however, information is only briefly documented in the literature (Fitch and Lavenberg 1975, Eschmeyer and Herald 1983), except for Marliave (1981) and Bailey et al. (1983) who reported the early life history in detail, and Allen and Smith (1988) who quantitatively illustrated aspects of its zoogeography.

These studies and our own observations, mostly in the northern Sea of Japan, enable us to compare life history traits of these fishes and to discuss probable life strategies associated with zoogeography. The notable fluctuation of the stocks of *A. japonicus* is also considered from the standpoint of comparative ecology.

Comparison between *Arctoscopus japonicus* and *Trichodon trichodon*

Distribution

The family Trichodontidae is restricted in distribution to the coastal boreal regions of the North Pacific between about 35°N and 60°N (Fig. 1). Although Schmidt (1950) reported the occurrences of *A. japonicus* from Akutan Bay and the vicinity of Sitka Island, in the Gulf of Alaska, these records seem questionable (Eschmeyer and Herald 1983). Perhaps these two species have distinct geographica ranges, separated by longitude 160–170°E. *Arctoscopus japonicus* occurs over an extensive area on the western side, including the offshore regions; it is extremely abundant in the Sea of Japan and the Pacific coast off Hokkaido, where catches amounted to 3.8×10^4 tons in 1968 (Ochiai and Tanaka 1986). *Trichodon trichodon* is an eastern Pacific form with a wider range from Kamchatka to southeast of San Francisco, California; there is no fishery for this species, but it is fairly common throughout the coastal waters (Hart 1973, Fitch and Lavenberg 1975, Eschmeyer and Herald 1983, Allen and Smith 1988).

Depth range is variable from the surface to about 400 meters in both species; however, the main life zones are slightly different for the two species. *Arctoscopus japonicus* in the Sea of Japan usually occurs at moderate depths of 200–300 m, with optimum

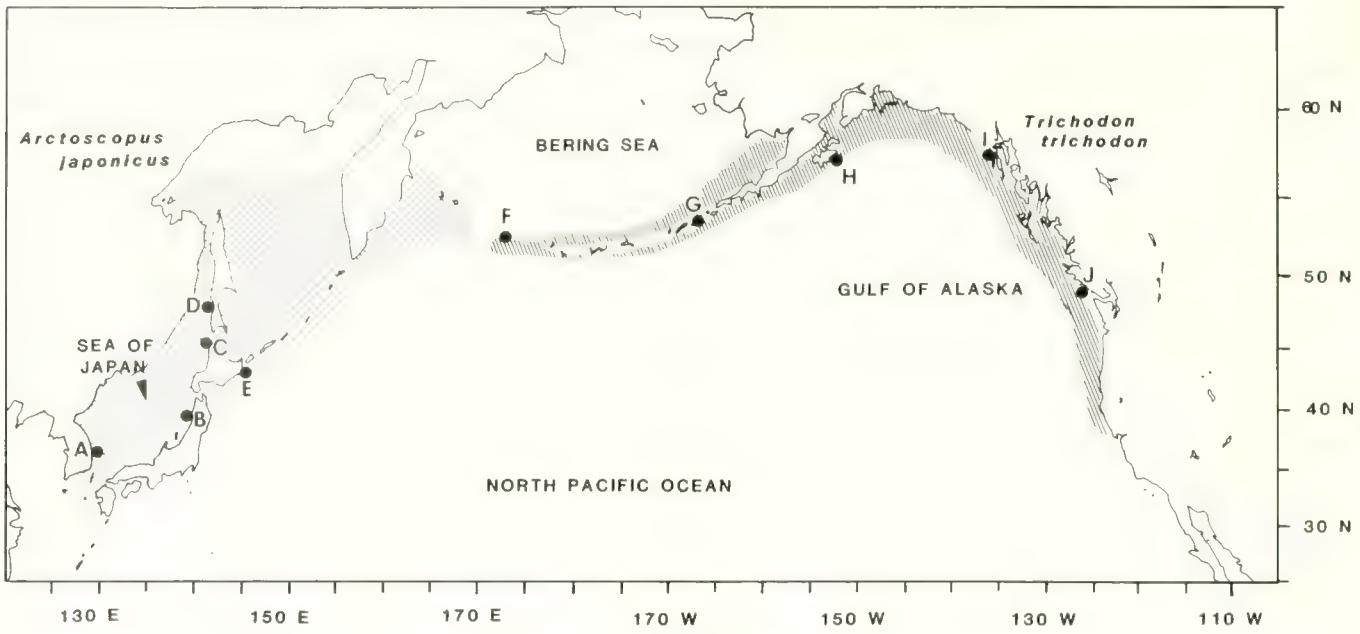

Figure 1

Geographical distribution of two species of sandfishes, family Trichodontidae. (A) Pohang, (B) Akita, (C) Wakkanai, (D) Kholmsk, (E) Nemuro, (F) Attu, (G) Dutch harbor, (H) Kodiak, (I) Sitka, (J) Vancouver. For references, see text.

temperature ranges of 2–5°C (Nishimura 1969). This zone is shifted to a shallower depth of 100–200 m on the Pacific side off Hokkaido (Ochiai and Tanaka 1986). During the spawning season, the adults move into water shallower than about 15 m. In contrast, *T. trichodon* is most frequent on the middle shelf at less than 150 m (Allen and Smith 1988) and spawning is restricted to the intertidal area.

Reproductive ecology

Both species spawn large demersal eggs in rocky, shallow waters during winter months, but interesting ecological differences are found between them, summarized in Table 1. Typically, *A.japonicus* deposits a spherical egg mass tightly on *Sargassum* spp. in such a way that supporting stems pass through the axis of the mass. Successful deposition of secure substrata is of prime importance for survival of eggs, because egg capsules that detach from the substrata become stranded ashore and perish. Onset of spawning at fixed times and locations is characteristic of *A. japonicus*. In the Akita district, for instance, the onset of spawning at major spawning sites rarely fluctuates beyond 1 or 2 weeks from the end of November (Kato 1980).

In contrast, Eschmeyer and Herald (1983) reported that the eggs of *T. trichodon* are laid in a gelatinous mass attached to rocks. One report of a natural spawning was on the wall of a fully exposed surge channel

Table 1

Comparison between reproductive characters of *Arctoscopus japonicus* and *Trichodon trichodon* (after Ochiai and Tanaka 1986; Marliave 1981, unless otherwise indicated below).

Characters	*A. japonicus*	*T. trichodon*
Spawning season	Mostly from the end of November to December	Around February
Spawning migration	Conspicuous	Indistinct
Spawning site; substrate	Coastal waters, 0–15 m depth; mostly *Sargassum* spp.	Intertidal waters, 0–1 m depth; rock
Shape of egg mass	Spherical, 3.3–7 cm in size	Irregular
Diameter of egg	3.3–3.5 mm*	3.52 ± 0.10 mm
Fecundity	600–2300	~1000
Incubation period	56–78 days at 6–9 C**	1 year (?) at 8–13 C
Synchronized hatching	No*	Yes; within 24 hours

*Okiyama (unpubl.)
**Maekawa (1985); this indicates the most frequent period.

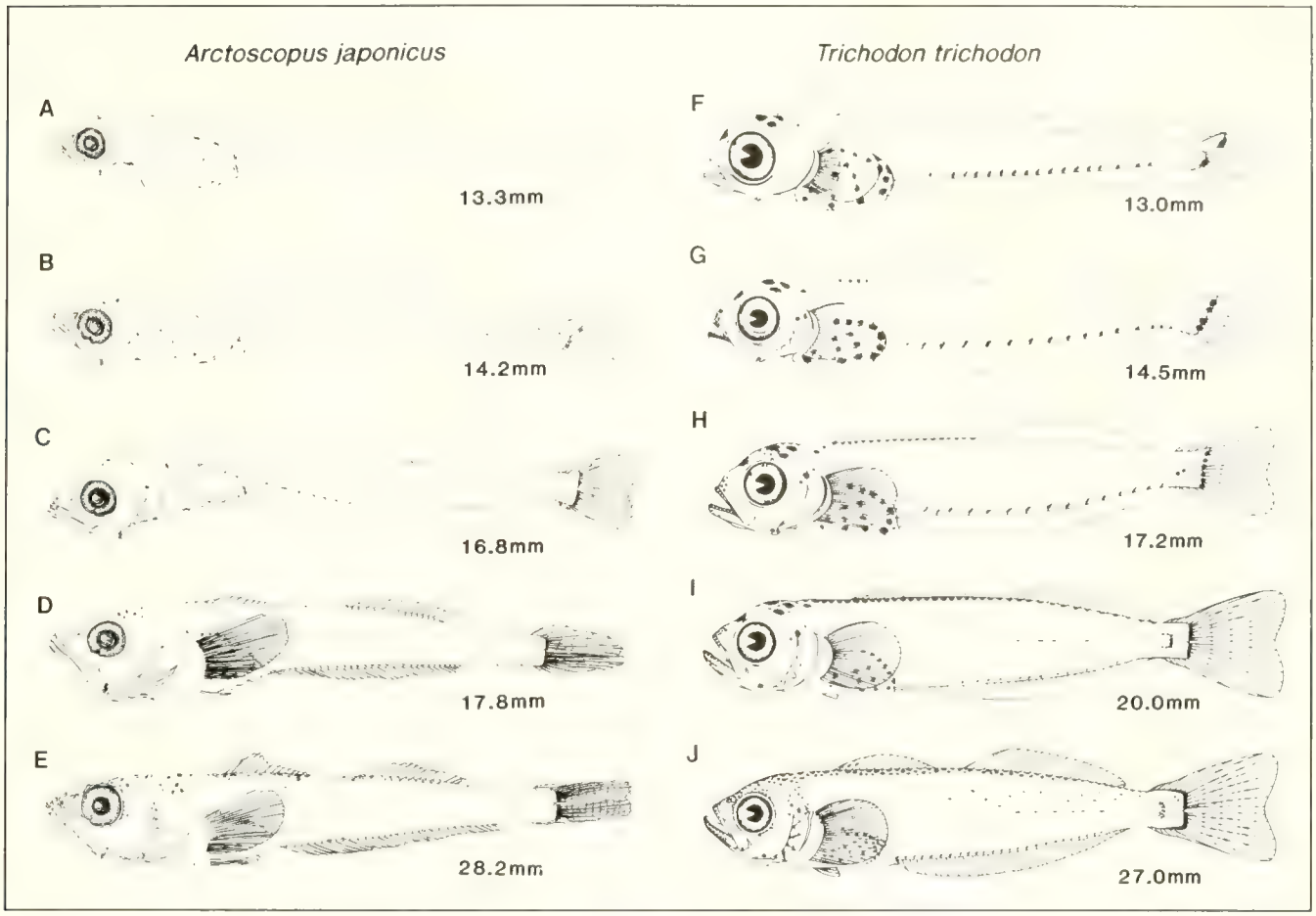

Figure 2

Comparison between early developmental stages of *Arctoscopus japonicus* (left) and *Trichodon trichodon* (right). Size in mm SL; preserved specimens (B–D after Okiyama 1988; F–J after Marliave 1981).

(Marliave 1981). It seems that *T. trichodon* selected this peculiar spawning location because it offered a refuge from egg predation as well as the high flow velocities necessary for respiration (Marliave 1981).

These contrasting reproductive styles should be associated with the different reproductive guilds proposed by Balon (1981, 1984). Although *A. japonicus* fits the "obligatory plant spawners" category, there is no guild relevant to *T. trichodon* within Balon's category of "nonguarders," suggesting its spawning habits may be unique.

Early life history

Larvae and juveniles of both species have been described and illustrated in detail from field and/or laboratory-reared materials (Marliave 1981, Okiyama 1988). In Figure 2, a series of early developmental stages of these species is reproduced from these references, with additional specimens of *A. japonicus* included. Here, specimens of similar sizes are selected to facilitate interspecific comparison. The early growth of the two species is also compared in Figure 3, based on the laboratory-rearing results; the comparison reveals that *T. trichodon* is consistently larger than *A. japonicus* throughout the 2 months following hatching (Marliave 1981, Maekawa 1985). Despite close resemblances in the general morphology, there are remarkable differences in early developmental patterns between the two species. A few interesting aspects are as follows:

(a) Newly hatched larvae of *A. japonicus*, 13 mm notochord length (NL), are less advanced than those of *T. trichodon*, 13.0 mm standard length (SL); the body is slender, the notochord tip is straight, and fin elements, except several incipient caudal rays, and teeth are absent. In contrast, *T. trichodon* possesses many precocious characters, including a flexed notochord with full complement of principal caudal rays, developing pectoral rays and preopercular spines, in addition to a deeper body, larger eyes, and the presence of

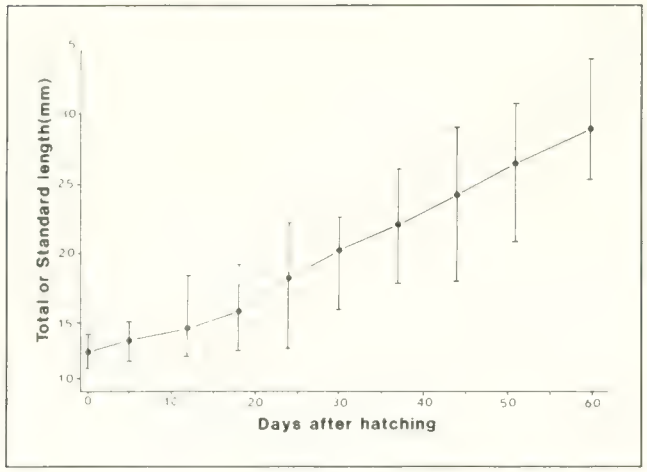

Figure 3

Early growth of laboratory-reared specimens of sandfishes in fresh condition. For *Arctoscopus japonicus*, average (●) and ranges (line) are shown in TL mm (after Maekawa 1985); for *Trichodon trichodon*, individuals (O) are shown in SL mm (after Marliave 1981).

Table 2

Comparison between fin formation of *Arctoscopus japonicus* and *Trichodon trichodon* (mm SL).

	*A. japonicus**		*T. trichodon***	
Characters	start	finish	start	finish
1st dorsal	16.2	19.0	20.0–	28.0
2nd dorsal	16.2	17.8	20.0	27.0
Anal fin	16.2	17.8	20.0	27.0
Pectoral	14.9	17.8	13.0	17.2
Pelvic	16.8	19.0	27.0	30.0
Caudal (principal)	14.9	14.9	13.0	13.0

*Original data from specimens of the Sea of Japan.
**After Marliave (1981), slightly modified on the basis of two newly hatched larvae (13.0, 13.2 mm SL; preserved) provided by him.

teeth on both jaws. It is clear that these precocious characters are mostly concerned with active swimming. Fast swimming, coupled with large sizes, would not only facilitate successful feeding, but would play an effective role in lowering predation pressure. Slight but distinct size and development differences at hatching between the two species, therefore, are among the most important aspects of their early life histories.

(b) Orders of fin ray ossification of the two species can be derived from Table 2, although the available size series of *T. trichodon* (Marliave 1981) is somewhat limited. Except for the precocious caudal and pectoral fins in *T. trichodon*, all other fin meristics are formed in smaller specimens of *A. japonicus*. The entire size ranges for fin development are 14.9–19.0 mm in *A. japonicus* versus 13.0–30.0 mm in *T. trichodon*. Possible sequence of fin ossification is caudal-pectoral-anal-2nd dorsal-1st dorsal-pelvic for both species.

(c) Larvae of both species are sparsely pigmented and lack extensive melanin on the lateral side of the tail. Pigmentation is generally heavier in *T. trichodon* than in *A. japonicus*. In particular, earlier development of distinct spots along the anterior dorsal margin of *T. trichodon* is remarkable because this character first occurs after transformation into juveniles in *A. japonicus*.

(d) According to the conventional definitions of early developmental stage, transformation from larval to juvenile stages occurs at about 20 mm in *A. japonicus* versus about 30 mm in *T. trichodon*. However, *T. trichodon* is distinctly more advanced than *A. japonicus* in every early-life-history trait, except formation of fins other than the caudal and pectoral.

Major contrasts in their ontogenetic properties may be summarized as follows: *A. japonicus* has a distinct, but truncated, metamorphosing phase (20–30 mm SL) closely corresponding to the change from pelagic to demersal life (Minami and Tanaka 1985, Okiyama unpubl.); in contrast, *T. trichodon* has a less distinct metamorphosing phase (30–50 mm SL) without any ecological shifts other than possible decrease of schooling tendencies (Marliave 1981, Bailey et al. 1983), although it starts burying itself in the sand at 55–60 mm SL (J.B. Marliave, Vancouver Aquarium, P.O. Box 3232, Vancouver, B.C., Canada, pers. commun., April 1989).

Contrast in life history strategy

Notwithstanding the close systematic relationship between *A. japonicus* and *T. trichodon*, there are many life history features unique to each species, particularly with respect to the reproductive styles as discussed earlier. The terms and duration of their early developmental stages are shown in Figure 4, revealing that the egg stage of *T. trichodon* is almost four times longer than that of *A. japonicus*; however, the time when the larvae of both species appear is restricted to the spring seasons. The mechanism of this synchronized hatching is unknown, but plausible advantages are apparent. It is obvious that spawning substrates play an important role in producing these contrasting patterns of development. Perhaps the specialized mode of egg deposition unique to *A. japonicus* has evolved in close association with the abundant substrates represented by *Sargassum* spp., whereas, as suggested Marliave (1981), most plant substrates would have been too transitory to act as an egg deposition site for *T. trichodon*.

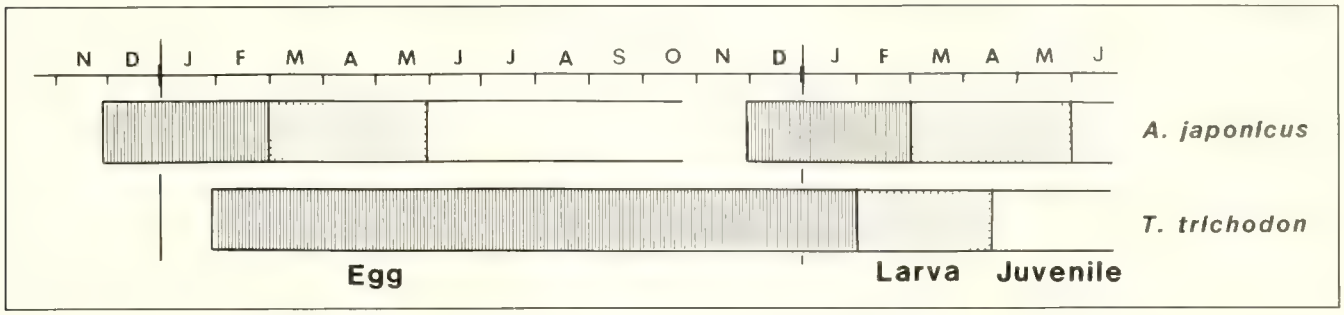

Figure 4
Comparison between terms and duration of early developmental stages of *Arctoscopus japonicus* and *Trichodon trichodon*. For sources, see text.

These ecological differences in spawning are compared with seasonal variations of the surface water temperatures among several stations covering most of the distribution areas of the two species (Fig. 5). By inspection, the location of two groups of stations may be recognized as corresponding to the zoogeography of the two species. Temperature ranges for *A. japonicus* are uniformly broader than those for *T. trichodon*: −2°-10°C to 18°-25°C versus 2°-7°C to 9°-14°C. Furthermore, temperature differences where the two species occur are particularly great during the warmer seasons. In the Sea of Japan, *A. japonicus* apparently copes with these extreme environmental conditions by precisely timing their early ontogeny to cold seasons and by gradually shifting the habitat toward deeper levels (up to 200–300 m) as growth proceeds (Nishimura 1969, Minami and Tanaka 1985).

Alternatively, the lowest temperature ranges of the eastern Pacific stations lie intermediate to those of the western Pacific stations. This stands in sharp contrast with the highest temperatures, which are not overlapping. Considering the year-round occurrence of the eggs of *T. trichodon* in the rocky intertidal area, it is quite natural to suppose that this species demands a particular set of physical environmental conditions for the specific spawning site, such as less variable water temperatures and above-freezing temperatures. These specific thermal conditions may also be responsible for the indistinct ontogenetic migration of *T. trichodon*.

Although there is no reliable information on the abundance of *T. trichodon*, except catch data of Allen and Smith (1988), *A. japonicus* surely has greater stocks than the former species. Total landings of *A. japonicus* in the Sea of Japan by Japanese vessels peaked at 3.3×10^4 tons in 1966. Of these, 2.1×10^4 tons were caught in the restricted area along the northwestern district of the Japanese mainland, namely, Akita Prefecture, where one of the biggest spawning grounds occurs regularly (Okiyama 1970, Kato 1980).

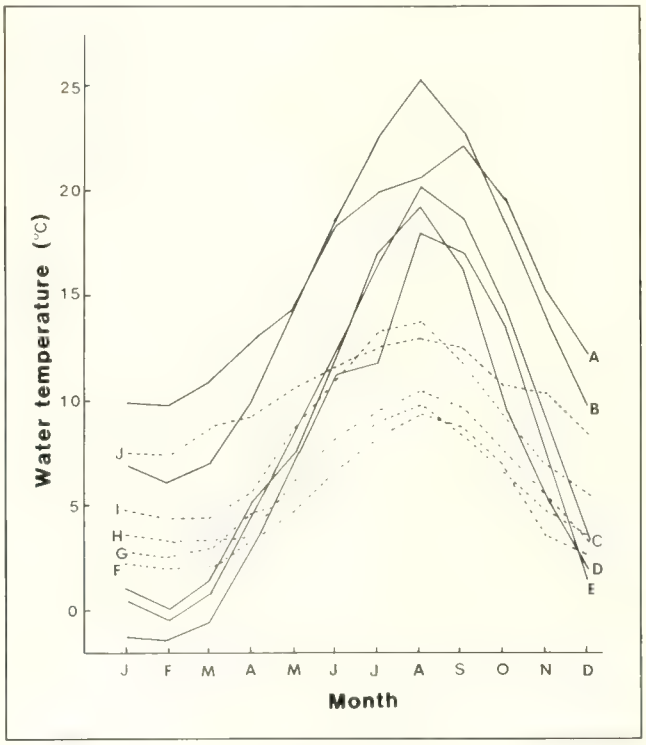

Figure 5
Seasonal patterns of surface-water temperatures from ten stations within the ranges of *Arctoscopus japonicus* (A–E, solid lines) and *Trichodon trichodon* (F–J, dotted lines) (adapted from Wadachi 1960). For locations, see Figure 1.

Figure 6 shows the long-term fluctuations of the catches of *A. japonicus* in this district. Coastal catches, comprised exclusively of fully matured specimens, are separated here from the total catches. Drastic changes in catches occurred during a 30-year period with peaks occurring around 1965–68 and 1974–75. The decrease between these peaks is slight as compared with the events in other periods such as around 1955 and after 1978. In 1984, the coastal catch dropped to a low of

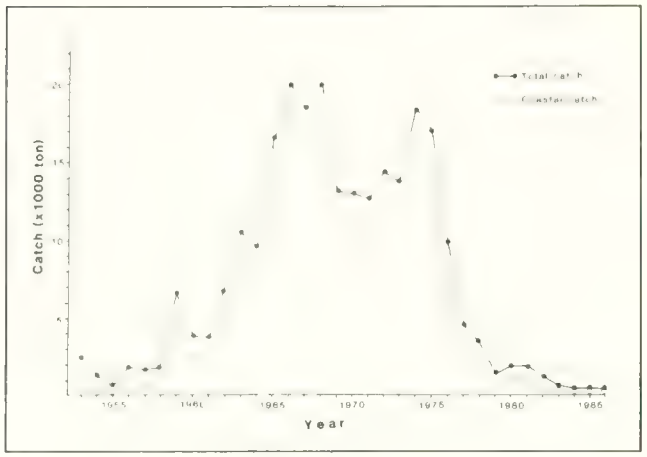

Figure 6
Fluctuation of the catch of *Arctoscopus japonicus* in Akita district, the northern Sea of Japan (after Ikehata 1987).

only 10^3 tons from the maximum record of about 18 000 tons in 1966; the maximum/minimum ratio was about 180. Such drastic fluctuations may be extremely rare among demersal fishes, and a ratio of about 180 would be exceptionally great even among pelagic fish stocks (Funakoshi 1988). Usually these fluctuations are attributed to heavy fishing on a parent stock after the appearance of several poor year-classes, or conspicuous recruitment success in particular periods (Lasker 1981). It is alo generally accepted that success or failure in survival during the early period of ontogeny is critically important for successful year-classes.

In addition to the early-life-history traits, rearing experiments suggest that early larvae of *A. japonicus* have many adaptive features promoting survival. They include an early onset of exogenous feeding paired with a long period of mixed feeding (mixed endogenous and exogenous feeding) in larvae 3 days after hatching to early juveniles of about 20 mm SL (Maekawa 1985). Likewise, Marliave (1981) observed an early onset of first feeding in *T. trichodon*, at about 48 hours after hatching in an aquarium. Prolonged mixed feeding is also possible in this species. This may suggest that starvation is not usually the main cause of mortality in early stages. Concerning other mortality factors, such as predation during the early larval period, no reliable information is available for either species.

The importance of mixed feeding as a feature of a developing organism was stressed by Balon (1986). He suggested that the flexibility provided by a varying duration of mixed feeding can facilitate changes in the entire life history of the species. In view of the characteristic mixed-feeding feature of early stages of these two species, their contrasting ontogeny seems to be largely explained within this context. Possibly, slight differences in size and yolk volume in newly hatched larvae of the two species are responsible for creating the observed dichotomy in their life history patterns: *A. japonicus* developed the indirect type of ontogeny, having a distinct pelagic larval stage and demersal juveniles with intervening metamorphosis; *T. trichodon* developed the rather direct type of ontogeny having no distinct pelagic larval stage.

These contrasting life history patterns may be closely associated with the probable differences of their stock sizes. For example, the highly derived nature of ontogeny in *A. japonicus*, including the locally restricted spawning grounds, the specialized spawning method, the remarkably precise spawning season, and the typical sequence of early developments, may imply a high likelihood of a greater sensitivity of stock size to environmental changes. Of these features, the presence of so-called "first metamorphosis" (Youson 1988) should be emphasized because this phase, although less drastic than than the others, is expected to play a significant role in regulating successful transition events according to varying environmental situations.

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Abstract.—The sublethal effects induced by a model carcinogen and environmental contaminant on salmonid emergence behaviors have been studied. Rainbow trout embryos were exposed for 24 hours to 25 μg/mL of benzo[a]pyrene 1 week prior to hatching. Exposures occurred during the late organogenesis period of development and allowed assessment of how a single embryonic exposure might affect emergence behaviors nearly 6 weeks later. Though no differences in numbers of alevins successfully emerging were observed, a significant decrease was noted in performance of the upstream orientation behaviors characteristic of emergence among wild individuals. These findings are discussed in terms of a model describing the role of upstream swimming behavior after emergence.

Decreased Performance of Rainbow Trout *Oncorhynchus mykiss* Emergence Behaviors Following Embryonic Exposure to Benzo[a]pyrene

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As aquatic ecosystems worldwide continue to function as ever-increasing reservoirs of environmental pollutants, the presence of many diverse classes of compounds is being documented (Champ and Park 1982). One class of compounds, the aromatic hydrocarbons, has been implicated in carcinogenesis in feral fish populations (Baumann 1989). Previous studies (Ostrander et al. 1988, 1989) and work presented here suggest that aromatic hydrocarbons may also exert subtle, yet profound, behavioral effects during early development.

Benzo[a]pyrene (B[a]P) is an aromatic hydrocarbon that is combustion product of organic materials (e.g., forest fires). Furthermore, anthropogenic activities have introduced significant amounts of B[a]P into the aquatic environment both directly (industrial emissions and oil spills) and indirectly (automobile exhaust and coal burning). This compound has been well studied in mammalian systems (reviewed in Gelboin 1980), and much is known of its mode of action. Recently we have verified the sensitivity of coho salmon early-life-history stages to a single embryonic exposure to benzo[a]pyrene (Ostrander et al. 1988). Embryonic exposure to B[a]P resulted in temporal differences in hatching, reduced and altered emergence success, and decreased foraging efficiency.

We next studied emergence behaviors following embryonic B[a]P exposure of the rainbow trout *Oncorhynchus mykiss*. We describe the effect of B[a]P exposure on the emergence success and upstream swimming behavior. A qualitative model, utilizing data from our rainbow trout and coho salmon studies, is proposed to explain the effects of toxicants on these early life behaviors.

Materials and methods

Experimental animals and exposures

Two replicates of a single experiment with rainbow trout were conducted with eggs obtained from the McCleary Trout Lodge, Tacoma, Washington.

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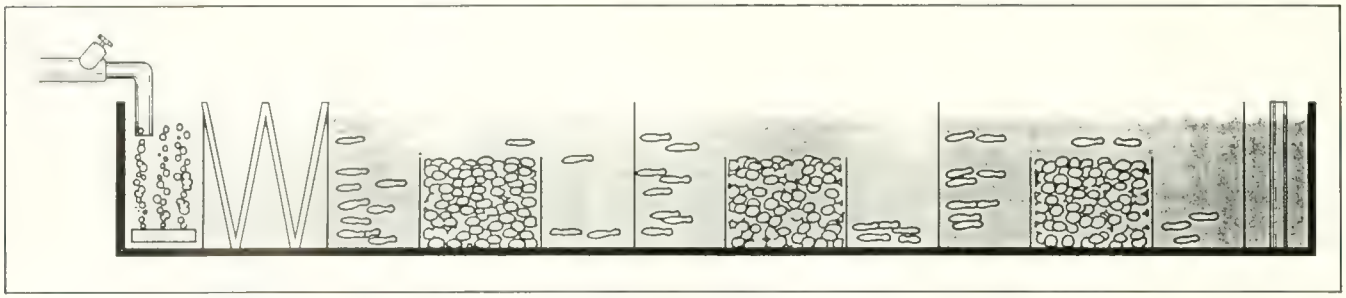

Figure 1

A single raceway containing three artificial gravel-filled redds and respective upstream and downstream compartments. Entering water was aerated and passed through a series of four baffles to reduce turbulence over the redds. Water exited through a standpipe at the opposite end of each raceway. Emerging fish, after entering either the upstream or downstream compartment, were removed and scored 3–5 times daily.

Eggs of a single female were fertilized with the pooled sperm of 12 males. Following fertilization, eggs were suspended in a continuous flow of lake water regulated with dechlorinated city water to a constant temperature of 12° ± 1°C. One week prior to hatching (late organogenesis), eggs were divided into three groups of 150 eggs and each group was transferred to glass petri dishes for a 24-hour exposure in a volume of 0.4 mL water per egg. B[a]P (Aldrich Chemical Co, Product #B1,008-0) was suspended in spectrophotometric grade DMSO (Schwarz/Mann Biotech, Product #820636) to make a stock solution of 10 mg/mL. This solution was diluted in lake water to make the final exposure concentrations of 25 μg/mL. The control groups were exposed to filtered lake water, the solvent control group was treated with 0.5% solution of dimethylsulfoxide (DMSO) in filtered lake water, and the exposure group was treated with 25 μg/mL of B[a]P in 0.5% DMSO in lake water.

Experimental apparatus

Artificial redds were constructed in replicate raceways by subdividing each raceway into ten compartments (Fig. 1). The upstream compartment contained baffles to reduce water turbulence in the redds. The remaining nine compartments included three redds (30 cm wide × 40 cm long) each occupying a single compartment and centered between an open upstream and downstream compartment (30 cm wide × 20 cm long). The redds consisted of smooth rocks (2–4 cm diameter) contained within perforated stainless steel plates. Adjacent open compartments were separated by plastic netting. The redd surface was within 8 cm of the water surface and the open compartments were 20 cm deep. The water, filtered to remove large particulates, flowed through each raceway at a velocity of 45 cm/second.

Following exposure, the eggs were rinsed with lake water and buried 8–10 cm deep in artificial redds. The position of the various groups in each raceway was randomized. The redds were maintained in darkness throughout embryonic development at a temperature of 12.0° ± 1°C. Beginning 60 days postspawning, the raceways were checked daily for emerged fry, and, following emergence of the first fry, the raceways were checked three to five times daily. Alevins emerged and held station above the redds while orienting against the water flow. After several minutes they would (1) swim into the upstream compartment, (2) swim into the downstream compartment, or (3) drift backward into the downstream compartment.

Data collection

The presence of an alevin in either the upstream or downstream compartment provided a quantitative measure of the ability of the fish to perform its typical upstream swimming behavior. Fish in the upstream and downstream compartments were counted and removed. Furthermore, 20 fry from the upstream and downstream compartments of each exposure group were randomly selected for measurements of total length, dorsal fin height, caudal fin height, pectoral fin height, anal fin height, and dry weight. An analysis of variance followed by a Student-Newman-Kuels multiple range test was used to test for significant differences among the means of the various exposure groups.

Results

Rainbow trout were exposed to a sublethal 24-hour pulse (25 μg/mL) of B[a]P during late organogenesis. The emergence success of rainbow trout treated with

Mention of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Emergence and upstream swimming behavior of rainbow trout and coho salmon, showing number of fish performing each behavior. In each experiment 150 apparently healthy salmon or trout eggs (embryos) were buried 1 week prior to hatching.

Replicate number	Fish species	Exposure group	Number emerged	Number upstream (% of emerged)	Number downstream
1	Rainbow trout	Control	136	103 (76)	33
		DMSO	138	104 (75)	34
		B[a]P	147	68* (46)	79
2	Rainbow trout	Control	139	115 (83)	24
		DMSO	145	115 (79)	30
		B[a]P	143	60* (42)	83
3[a]	Coho salmon	Control	148	132 (89)	16
		DMSO	142	115* (81)	27
		B[a]P	118**	76** (64)	42
4[a]	Coho salmon	Control	147	137 (93)	10
		DMSO	150	105* (72)	45
		B[a]P	103**	70** (68)	33

[a] Data from Ostrander et al. 1988.
* Significantly different from control group at $P<0.05$, chi-square analysis.
** Significantly different from control group at $P<0.001$, chi-square analysis.

Table 2

Morphological development of rainbow trout alevins at emergence. Values are means and ranges for groups of 20 fish.

Group	Total length (mm)	Dry body weight (mg)	Caudal fin height (mm)	Dorsal fin height (mm)	Pectoral fin height (mm)	Anal fin height (mm)
Upstream control	24.29 (22.6–25.6)	44.09 (43.9–44.4)	4.53 (3.8–5.0)	1.86 (1.5–2.2)	2.52 (2.2–3.2)	1.67 (1.4–2.0)
Downstream control	24.13 (21.5–25.1)	44.61 (44.4–44.9)	4.85 (4.0–5.6)	1.86 (0.8–2.3)	2.85 (1.9–3.3)	1.80 (0.8–2.1)
Upstream DMSO	24.41 (23.1–25.2)	44.47 (44.2–45.1)	4.69 (3.9–5.2)	1.80 (1.5–2.3)	2.96 (2.6–3.3)	1.80 (1.5–2.1)
Downstream DMSO	24.02 (21.4–24.9)	44.52 (44.3–44.8)	4.91 (4.3–5.4)	1.90 (1.4–2.3)	2.87 (1.8–3.3)	1.79 (1.4–2.1)
Upstream B[a]P	24.19 (21.4–25.5)	44.17 (43.9–44.5)	4.53 (3.8–5.4)	1.75 (0.8–2.1)	2.59 (1.9–3.3)	1.63 (1.4–2.3)
Downstream B[a]P	24.17 (23.3–24.9)	44.33 (44.1–44.6)	4.56 (4.0–5.2)	1.96 (1.6–2.4)	2.63 (2.3–3.0)	1.77 (1.4–2.1)

B[a]P was not significantly different (χ^2, $P<0.05$) from embryos treated with DMSO (solvent controls) or filtered lake water controls (Table 1). In both replicates more than 95% of B[a]P-exposed fish successfully emerged.

The two B[a]P-exposed groups, however, exhibited a decreased tendency to orient upstream when compared with DMSO or untreated controls (χ^2, $P<0.001$). Normal upstream orientation observed among emerged untreated and DMSO solvent controls was 75–83% of emerging alevins, while among B[a]P-treated groups less than 46% of the emerged alevins reached the upstream compartment (Table 1).

Measurements of total body length, dry weight, and caudal, dorsal, pectoral, and anal fin heights are summarized in Table 2. There were no significant differences in the morphology of upstream and downstream fish or between respective groups when tested with a one-way analysis of variance.

Discussion

The salient result of these studies is that both rainbow trout and coho salmon exposed as embryos to a sublethal dose of B[a]P exhibit decreased ability to swim upstream after emergence from artificial redds.

Emergence and orientation are activities that terminate a sequence of early-life behaviors critical for salmonid survival. Following hatching, developing salmonid eleutheroembryos remain in gravel redds for 2–4 months until yolksac absorption and fin development are nearly complete (Fast 1987). As yolksac reserves are exhausted the eleutheroembryos migrate, primarily at night, to the upper layers of the redd. Emergence is complete when eleutheroembryos, now called fry, leave the redd and swim to the water surface to inflate the air bladder and begin feeding. The direction in which emergent fry migrate is species-specific. Coho salmon and rainbow trout fry typically orient and swim upstream to counteract downstream transport and to colonize natal and nearby streams unavailable to, or not used by, spawners (Mason 1976). Soon after emergence, fry establish and defend territories as feeding begins (Chapman 1962, Mason and Chapman 1965).

Our previous work (Ostrander et al. 1989) demonstrated that the lipophilic nature of B[a]P coupled with the expansive yolksac reserves of the embryo resulted in significant uptake of the compound and, furthermore, the B[a]P was only gradually lost from the egg throughout development. We found that over 60% of the B[a]P is retained in the eleutheroembryo at hatching when this exposure regimen is utilized. Consequently, rather than exposing our B[a]P-treated fish to an acute 24-hour pulse of B[a]P, they faced continuous exposure to B[a]P and its harmful metabolites (Gelboin 1980) as they exhausted their yolk reserves throughout early development.

There were no significant differences in numbers of fish emerging among the various control and exposure groups. Yet, fewer rainbow trout exposed to B[a]P as embryos exhibited typical upstream swimming behavior following emergence. These results are similar to previous findings for coho salmon (Ostrander et al. 1988). In that study, however, significantly fewer coho salmon, successfully emerged (Table 1). Perhaps the larger size of the coho alevin coupled with compromised abilities due to B[a]P exposure resulted in reduced success in negotiating the intersticial spaces of the redd during emergence. Fish in the downstream compartment did generally appear less active than fish in the upstream compartment. In neither study, however, were significant differences in weight or fin development among control and treatment groups observed, nor were any morphometric differences detected between fish going upstream or downstream in the experiments.

In these experiments, fish emerged from the gravel and oriented into the water flow. After about 1 minute, the majority of fish moved into the upstream compartment of the test apparatus. A smaller number of fish, generally less active, either swam or drifted into the downstream compartment. Successful upstream movement requires that the time to travel the distance across the redds is less than the time to become fatigued, assuming that fish in the downstream compartment became fatigued before they reached the upstream compartment. This is expressed, $T_f > T_t$, where T_t is the travel time to the upstream compartment and T_f is the fatigue time of the fish. Travel time to the upstream compartment depends on the average velocity of the current across the redds, U, the average fish swimming velocity, V, and the distance, L, it travels across the redd, and is expressed:

$$T_t = L/(V - U).$$

Fatigue time also depends on swimming velocity. Laboratory experiments indicate that among adult rainbow trout, the time to fatigue decreases exponentially with swimming velocity for velocities above 3 body lengths per second (bl/s). However, at 2 bl/s adult rainbow trout can swim indefinitely (Beamish 1978). Alevins probably have a similar relationship, although (due to smaller size) they can maintain considerably larger swimming velocities on a body length basis, exceeding 30 bl/s (100 cm/s) (Ostrander et al. 1989). The model assumes time to fatigue is infinite when swimming velocity is zero and decreases as swimming velocity increases. A simple power function has these properties:

$$T_f = k\ V^{-a}$$

where k and a are parameters that depend on condition of the environment and the fish. Equating the two time scales, a critical stream velocity is defined:

$$U^* = V - L/kV^a$$

where successful upstream migration requires $U < U^*$. The intersection of U and U^* defines a swimming velocity range required for successful movement into the upstream compartment (Fig. 2). For velocities outside the allowable range fish become fatigued before they reach the upstream compartment.

The experiments indicated that fish exposed to B[a]P had a greater chance of ending up in the downstream compartment. This result could be achieved if fish

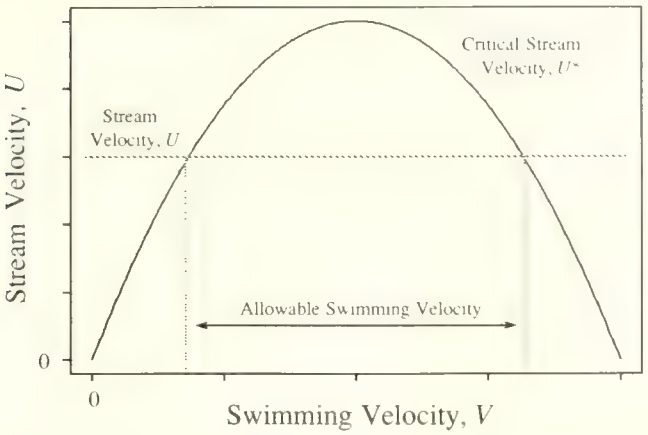

Figure 2

Critical stream velocity curve. Successful upstream movement requires that the critical stream velocity is greater than the stream velocity. Intersection of U and U^* defines the allowable swimming velocity, V, required for successful movement into the upstream compartment.

exposed to B[a]P became fatigued faster or swam upstream slower. In the first case, the critical stream-velocity curve of exposed fish would fall below the curve for unexposed fish. In the second case, the lower swimming velocity of the exposed fish would fall outside the allowable velocity range for successful upstream migration. The experiments were not designed to resolve such differences.

The model provides a qualitative basis for interpreting the experiments. It differs from standard dose-response models that describe the degree of change as a continuous function of the level of duration of toxicant exposure (Krewski and Brown 1981). The model allows a possible interplay of behavior and stamina for successful upstream movement, although such a separation was not pursued in the study.

Our results indicate that low levels of toxicants may affect important early-life-history behaviors critical to survival. Though the concentration of B[a]P used in this study is not frequently encountered in nature, the value of this study in predicting what could happen following some type of major accidental spill or discharge should not be overlooked. Given that a single 24-hour pulse of B[a]P elicited significant behavioral changes, future studies could be directed at understanding the potential effects of low-level chronic exposures which may more accurately mimic natural conditions.

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Abstract.–Sagittal otoliths of the Antarctic fish *Nototheniops nudifrons* (Family Nototheniidae) contain internal microincrements which are visible by scanning electron microscopy. Microincrements were deposited on a daily basis, as validated through tetracycline and acetazolamide marking experiments. This was the first validation of daily microincrement deposition for any Antarctic fish. Daily formation of microincrements continued throughout the year, including during the winter when daylight periods were short. Counts of daily microincrements in the otoliths of 32 juveniles and adults allowed the determination of age and growth rates. From this sample, a multivariate regression model relating fish age to otolith morphometrics and fish size demonstrated that age could be estimated reliably from sagittal otolith weight and length. Age was estimated for a large sample of *N. nudifrons*, which allowed the determination of growth and natural mortality. Fish grew slowly (15 mm per year), reaching sexual maturity at an age of 4–5 years, with the largest fish attaining ages of more than 8 years. Growth and survivorship were similar for males and females.

Age and Growth of the Antarctic Fish *Nototheniops nudifrons**

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The Antarctic fishes are characterized by a high degree of endemism and extensive adaptations to their unique environment (DeWitt 1971). Although commercial exploitation of several species has begun, much of their basic biology is still poorly understood (Kock et al. 1985). Of special importance to ecological and fisheries research is determination of the age of fish captured in the field. Growth, mortality, and fecundity can be derived from age data. Ageing studies can also provide basic life-history information, such as population structure, and changes in population growth due to environmental perturbations. These age-related data increase our understanding of fish biology and form the basis of population dynamics models.

Antarctic fishes appear to be slow growing and long lived (Shust and Pinskaya 1978, Freytag 1980a, Kock et al. 1985, Radtke et al. 1989). Although age and growth of Antarctic fishes have primarily been determined by counting scale annuli (Olsen 1954, 1955; Wohlschlag 1961, 1962; Everson 1970, 1980; Shust and Pinskaya 1978; and others), the results from this technique are often difficult to interpret and especially unreliable for older fishes, as scales may be regenerated or resorbed (Mugiya and Watabe 1977; Freytag 1980a, 1980b). Therefore, an alternative ageing method, such as otolith increment analysis, is desirable. In contrast to scales, otoliths are neither regenerated nor resorbed, and are the most precise structure for ageing of fishes (Six and Horton 1977, Campana and Neilson 1985).

Otoliths are calcium carbonate structures deposited in the membranous labyrinth of the inner ear of fish. The otoliths of many fishes grow by daily accretion of layered increments (Pannella 1971). These increments are visible in sectioned otoliths as concentric rings, which can be enumerated to provide estimates of the age of temperate and tropical fishes (Pannella 1971, 1974; Campana and Neilson 1985; Jones 1986). Otoliths of temperate fishes may also form annual increments or annuli.

Several studies have utilized otoliths to age Antarctic fishes. Olsen (1955) found that the otoliths of icefishes were small and difficult to analyze by light microscopy. Rings in the otoliths of the icefishes *Chaenocephalus aceratus* and *Champsocephalus gunnari* were interpreted to be annuli (Olsen 1955). Subsequently, other researchers used rhythmic patterns in Antarctic fish otoliths for age determinations (Hureau 1966, Everson 1980, Freytag 1980b, North et al. 1980, Mucha 1980, Chojnacki and Palczewski 1981, Kock 1981,

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Sosinski 1981, Kochkin 1982, Burchett et al. 1984). These patterns were interpreted to be annuli; however, no validation data were available for the deposition rates of these increments. These presumed annuli, which are often difficult to discern and interpret, may not represent yearly growth increments (Scherbich 1975, Freytag 1980b, Radtke and Targett 1984).

Townsend (1980) described the presence of microstructural growth increments in Antarctic fish otoliths. These increments appeared to be analogous to the daily increments found in a host of fish species (see review by Campana and Neilson 1985). Such microincrements were used by Radtke and Targett (1984) to age *Notothenia larseni*, and are the foundation for the present research. However, the daily or annual nature of rhythmic patterns in otoliths has not been experimentally validated for any Antarctic fish species. Microincrements may generally form in response to changes in daily periods of light and dark (Radtke 1984), suggesting that special problems may exist in the formation of daily increments during times of short daylight in the winter months.

Management programs for Antarctic fisheries require knowledge of population parameters of both commercial and sympatric, non-commercial, species. *Notothenios nudifrons* (=*Notothenia nudifrons*) is among the most abundant demersal fishes in many habitats of the Antarctic Peninsula (DeWitt 1971). As such, this species may play a major role in the trophic structure of the Antarctic marine community, both as competitor with and prey for commercial species.

We recently reported on the reproductive biology of *N. nudifrons* (Hourigan and Radtke 1989). In the present study, the age and growth of *N. nudifrons* were determined by the examination of microincrements in sagittal otoliths. Microincrement deposition rates during different seasons were tested under experimental conditions. Correlations of age to otolith morphometrics allowed ageing of a large sample of fish and an estimation of their natural mortality rates.

Methods

Collection of fish and initial measurements

A total of 32 *Notothenios nudifrons* were collected on 28 March and 17 April 1985 by otter trawl in 54–110 m depths off Low Island (63°24′S to 63°27′S; 62°07′W to 62°17′W). An additional 30 fish were collected in the same area in February 1984, and used for preliminary otolith validation studies. All individuals were transported live to Palmer Station and placed in tanks with flow-through seawater. In addition to these fish, scuba divers collected three small juveniles near Palmer Station in Arthur Harbor (64°46′S; 64°04′W) in May and July 1985.

The fish from the 1985 trawls were analyzed for length-weight relationships and growth. Standard length (SL) and total length (TL) were measured to the nearest millimeter. Whole body weights were measured to the nearest 0.001 g. Otoliths were removed from all fish, cleaned, dried at 60°C, and stored in a desiccator. The gonads were examined to determine sex and reproductive condition (Hourigan and Radtke 1989).

The remaining fish were injected intramuscularly with acetazolamide (samples from 1985 only) or tetracycline (samples from 1984 and 1985) and kept in 500-L tanks with flow-through seawater, at ambient temperatures and natural photoperiods. Ten fish were kept in each tank, along with 10 *Notothenia gibberifrons*. Rocks were added to the tanks to provide shelter and nesting sites. Fish in tanks were fed *ad libitum* with krill every 2 days.

Fish were kept alive for a maximum of 158 days after injection, from April to October, at which time they were sacrificed, weighed, and measured. Otoliths of these fish were removed, cleaned, and stored dry in vials.

Otolith structure and age determination from otolith microincrements

To determine the relationship of age to otolith size and shape, the length, width, and weight of sagittal otoliths were measured. Otoliths were segregated according to their lateral position in the cranium. Left and right sagittae from all fish were scanned using a computer-aided video digitizer, which produced a measure of maximum length (from the rostrum to antirostrum; nomenclature of Hecht 1978) and width (the widest distance in the dorsal-ventral plane). Otoliths were weighed on a microbalance to the nearest 0.01 mg.

A sample of 32 fish (from fish collected in 1985) was chosen for age determinations. This sample was composed of males and females of a representative size distribution. Left sagittae from these fish were attached to scanning electron microscope (SEM) viewing stubs with epoxy, carefully ground down to the central area by hand using a fine sharpening stone, and then polished with 0.3-micron alumina paste. The polished surfaces were etched for 1–20 minutes with 6% ethylene diamine tetraacetate (EDTA) with pH adjusted to 8 with NaOH. After etching, the sections were gently washed with water, dried, coated with gold, and viewed by SEM at various magnifications (50–10 000×).

Otoliths were examined for microincrements. A microincrement was defined as an unbroken incremental zone with discontinuous zones as boundaries (Radtke and Dean 1982). Sequential etching made it

feasible to enumerate all increments. Individual sections were etched for different lengths of time, with 15–20 minute etching times showing the inner increments most clearly, and shorter etching periods revealing the outer increments. Landmark scratches were placed on each section with an insect needle to follow increments uncovered by different etching times. The otolith was etched in steps of 1 minute and viewed with the SEM after each etching to follow the progression of the smallest increments found. Examination of the three-dimensional microstructure of the left sagitta demonstrated that the midtransverse plane was the best plane for routine sectioning.

Validation of otolith ageing technique

Microincrements are generally assumed to be deposited daily (Pannella 1971, 1974; Radtke and Dean 1982; Radtke and Targett 1984). To test this, individual fish were given a single intramuscular injection of either tetracycline hydrochloride or acetazolamide at 0.025 mg/g body weight. Tetracycline is incorporated into the otolith and, viewed under a compound microscope with filtered reflected wavelengths of 700–800 nanometers, appears as a fluorescent band inside the otolith. Tetracycline marks are not visible by SEM. Acetazolamide is a carbonic anhydrase inhibitor which temporarily inhibits the calcification processes in the otolith resulting in a disruption band which can serve as a reference location for SEM study (Mugiya and Muramatsu 1982, Radtke unpubl. data).

Left sagittae from the fish injected with tetracycline were embedded in epoxy-casing resin and serially sectioned using a low-speed saw. The sections were polished as above, placed in nonfluorescent immersion oil, and examined under reflected ultraviolet light through a compound microscope. Otoliths with acetazolamide marks were prepared for SEM analysis as described above. The number of microincrements from the reference mark to the margin of the otolith was compared with the number of days between injection and the day that the fish was sacrificed.

Relationship of otolith dimensions and fish age

In an effort to determine other predictors of age in *N. nudifrons*, the data generated from otolith and fish measurements were applied to the multiple regression model:

$$\text{Age} = a + b_1x_1 + b_2x_2 + b_3x_3 + b_ix_i$$

In this model, age in years was determined by counting microincrements, a = intercept, b = regression coefficients, x = variables. The data were checked for normality, and the multiple regressions were determined in a stepwise fashion with the inclusion level for variables set at $p = 0.05$. As a measure of the variance associated with the otolith morphometric procedure, the percent of the total variance component due to variance between age estimates from the left and right sagittae of the same fish was calculated. Less than 5% of the total variance was due to variance between sagittae of the same fish (Table 1).

Table 1

Variance component due to within-fish variance in ages of *Nototheniops nudifrons* predicted from left and right otolith measurements, compared with variance among fish.

Variance source	df	Sums of squares	Mean component	Variance	Percent
Between fish	200	341.24	1.71	0.96	95.87
Within fish	200	6.08	0.04	0.04	4.13
Total	400	347.32	1.00	1.00	100.00

Results

A total of 216 *Nototheniops nudifrons* were collected in trawls off Low Island. Five were caught during six deep trawls in 100–110 m depth, with the remaining fish caught in four shallow trawls at depths of 54–80 m. Fish captured in trawls ranged in size from 70 to 149 mm SL. More females ($N = 127$) were collected than males ($N = 74$), and the modal size of females (100 mm SL) was slightly larger than that of males (90 mm SL; Fig. 1). Three smaller juveniles (each 45 mm SL) were collected by hand in 10 m depth at Arthur Harbor.

Length-weight relationships

Length-weight relationships of males and females are shown in Figure 2. Separate regression equations were calculated for males and females using a gonad-free body weight. Weight was approximately a cubic function of length, indicating nearly isometric growth. The length-weight relationship of the fish conformed to the power curve model Weight = $a(\text{SL})^b$. An analysis of covariance indicated that the slopes of the length-weight relationships for the sexes were not significantly different (df = 1, 203; $F = 2.30$, $0.05 < p < 0.25$). The conversion of standard length (SL in mm) to total length (TL in mm) was:

$$\text{TL} = 1.136(\text{SL}) + 1.529;\ (N = 216;\ R^2 = 0.99).$$

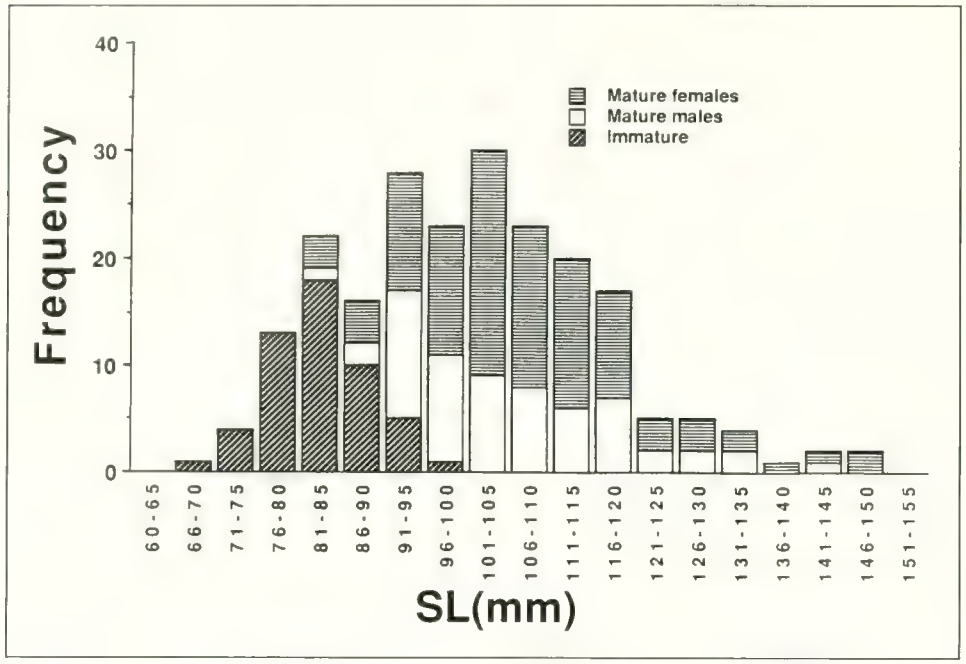


Figure 1
Length-frequency distribution of immature and sexually mature male and female *Nototheniops nudifrons* captured by trawls near Low Island in 1985.

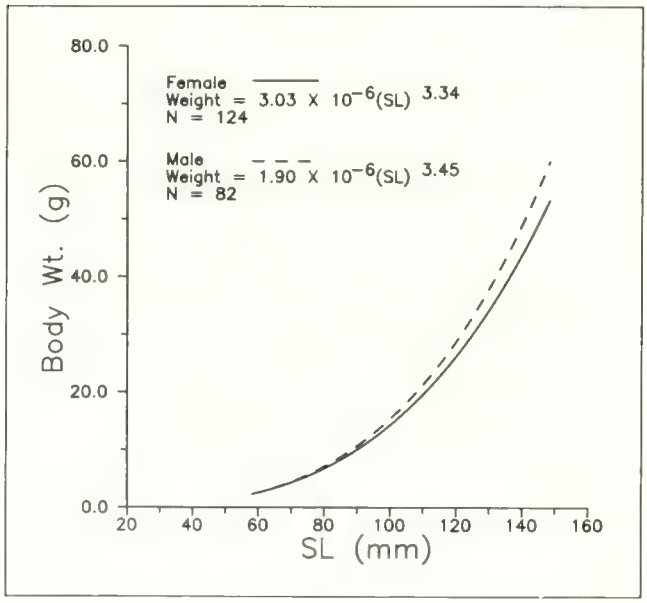


Figure 2
Length-weight relationship of male and female *Nototheniops nudifrons*. Wet body weight (with gonads removed) increased approximately as the cube of fish standard length (SL).

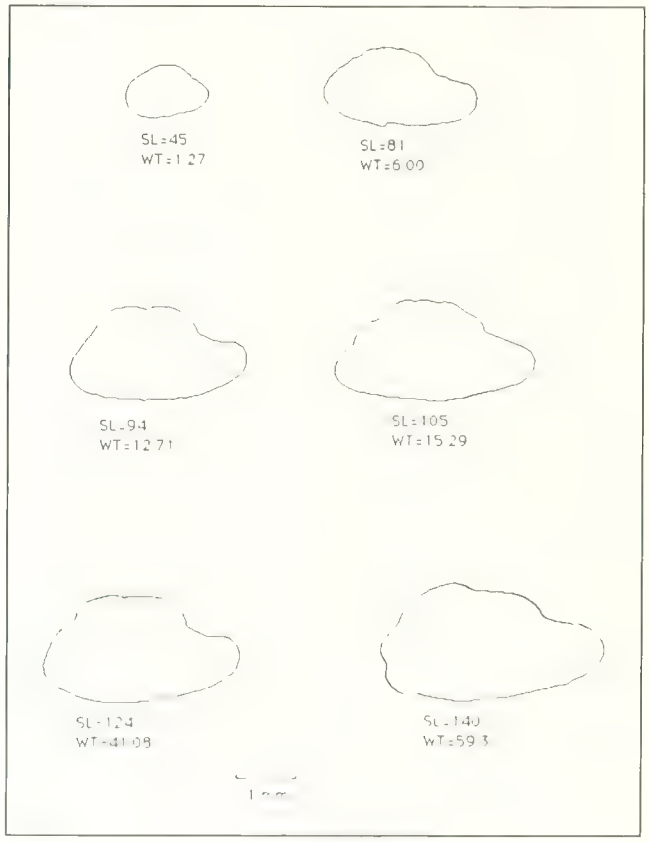


Figure 3
Change in size and shape of sagittal otoliths of *Nototheniops nudifrons* with increasing fish size. SL = standard length; WT = wet weight of fish.

Description of otoliths

The sagittae of *N. nudifrons* were large and oval in shape (Fig. 3) with a well-defined rostrum. The size of the rostrum was directly proportional to fish size. The external surface was smooth and gently rounded. Sagitta length was related linearly to fish length (SL)

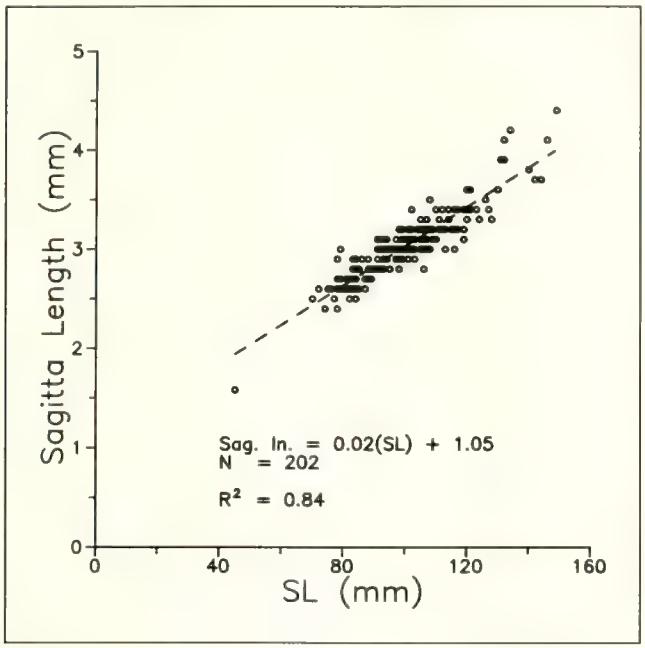


Figure 4
Relationship of sagittal otolith length to fish standard length (SL) for *Nototheniops nudifrons*.

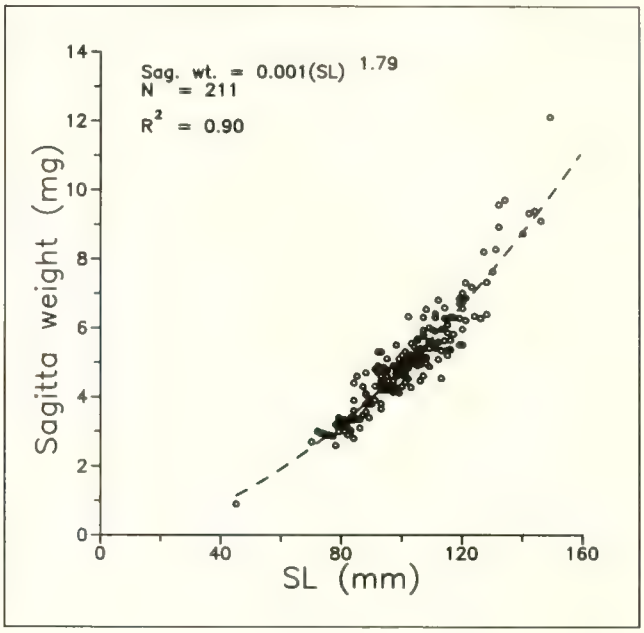


Figure 5
Relationship of sagittal otolith weight to fish standard length (SL) for *Nototheniops nudifrons*.

(Fig. 4), and sagitta weight was related exponentially to fish length (SL) (Fig. 5). Ground, polished, and decalcified sagittae were examined by SEM. A low magnification view of a sagittal otolith (Fig. 6) shows increments occurring concentrically from the center to the edge. Larger incremental patterns, or bands, were observed, but they could not be attributed to any specific environmental cues. Counts of microincrements within these bands showed that they were not true annuli. Sagittae exhibited a well-defined central core region or nucleus (Fig. 7a). Within the core region were concentric microincrements separated from the surrounding otolith by a distinct transition zone (Fig. 7b). Surrounding the core area were mineral crystals in a protein matrix which formed microincrements (Fig. 8a and 8b). Counts of microincrements were made beginning at the core transition zone and ending at the outer edge of the otolith. These microincrements varied in width from about 2 μm (Fig. 8a) to less than 1 μm (Fig. 8b). Differences in increment width may reflect periods of differential growth.

Validation of the daily nature of microincrements

The periodicity of growth increment formation was examined using tetracycline- and acetazolamide-marked specimens which were held in tanks at ambient light and temperature regimes after injection. After injection of tetracycline or acetazolamide, *N. nudifrons* displayed some evidence of short-term stress, including cessation of feeding for 2 or 3 days, but only one mortality occurred. Subsequently, the fish survived well in captivity, with 80% of all fish surviving the whole winter. Sagittae of 29 fish injected with tetracycline in February and March 1984 and held 4–34 days under natural daylight photoperiods were examined for post-treatment increments. A discrete fluorescent band was discernible in all specimens, and increments between the band and the margin of the otolith were counted (Table 2). The number of increments averaged 2.5 increments less than the number of days after injection. This difference corresponded well to the initial period of stress, and did not change with length of the experiment (Median test, $0.2>p>0.1$; Siegel 1956). Linear regression analysis (Model I, Sokal and Rohlf 1969) indicated that the slope ($b = 1.076$, 95% CI of 0.756–1.396) was not significantly different from 1 (Table 2). The y-intercept equaled −3.27 (95% CI of −7.73–1.19).

Sagittae from five fish injected with acetazolamide in April 1985 were examined by SEM. A discrete disruption of increments caused by the interruption of calcium deposition was discernible (Fig. 9). The number of increments from this disruption mark to the otolith margin averaged 9.2 increments less than the number of days after injection (Table 2). Acetazolamide disrupts metabolic processes and its effects can be expected to last longer than the tetracycline's, since the latter does

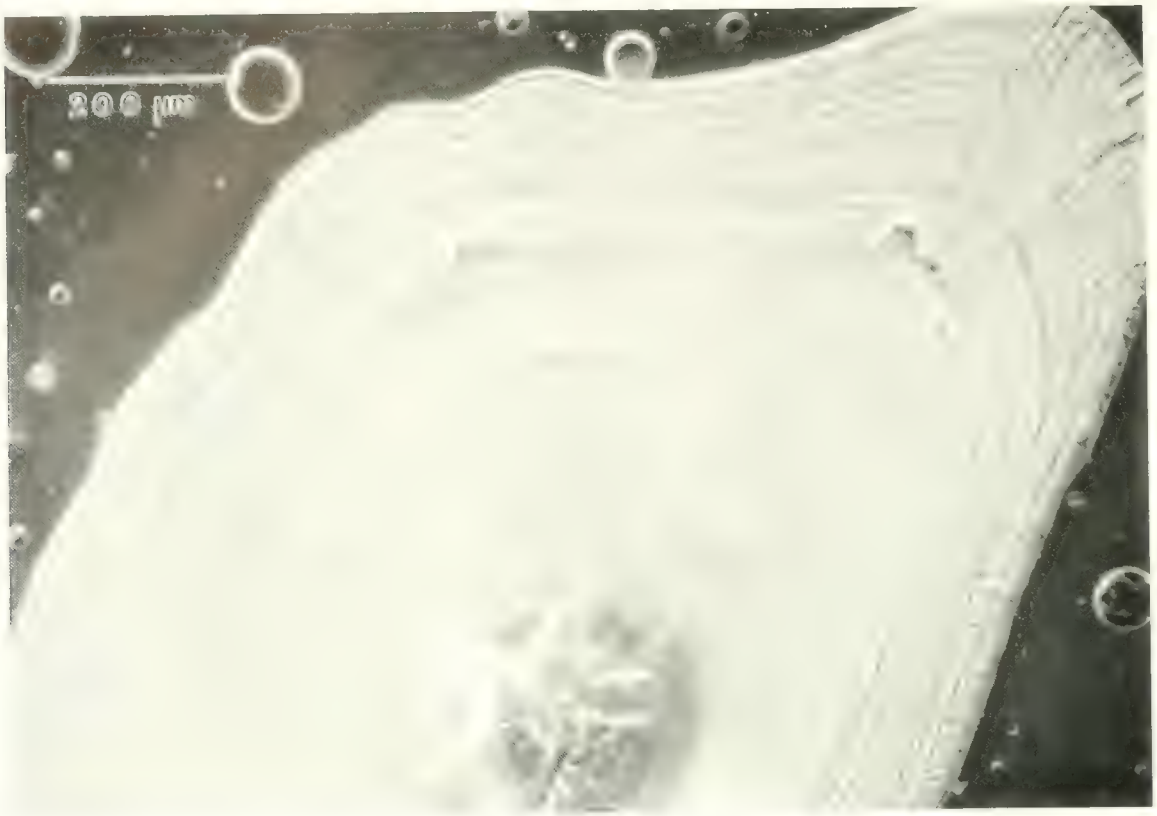


Figure 6

Low-magnification scanning electron micrograph of a sagittal otolith of *Nototheniops nudifrons*, showing concentric incremental patterns. The sagitta is from a 100-mmSL specimen.

not appear to affect the fish's metabolism. Linear regression results indicated a slope of 0.962 (95% CI of 0.983–0.941) and a y-intercept of −5.40 (95% CI of −2.80 to −8.01). The significance of this analysis is suspect because of the small sample size ($N = 5$). The discrepancy between postinjection days and microincrements counted increased from 5 to 12 with length of incubation period. However, this apparent increase in the discrepancy represents an actual percentage decrease in error from 50% to less than 10%. The longest incubation period in the acetazolamide experiment was 158 days, which was three times longer than the longest tetracycline incubation. This may explain why in the tetracycline experiment we did not observe an increase in the discrepancy between number of increments and days after injection.

During the experiment, the photoperiod varied from 9:15 hours Light:Dark, to a minimum of 5:19 L:D in June, to 15:9 L:D in October. The microincrements formed during incubation were uniform. Despite considerable variation in photoperiod, we found no indication that microincrements cease to form on a daily basis.

Age and growth

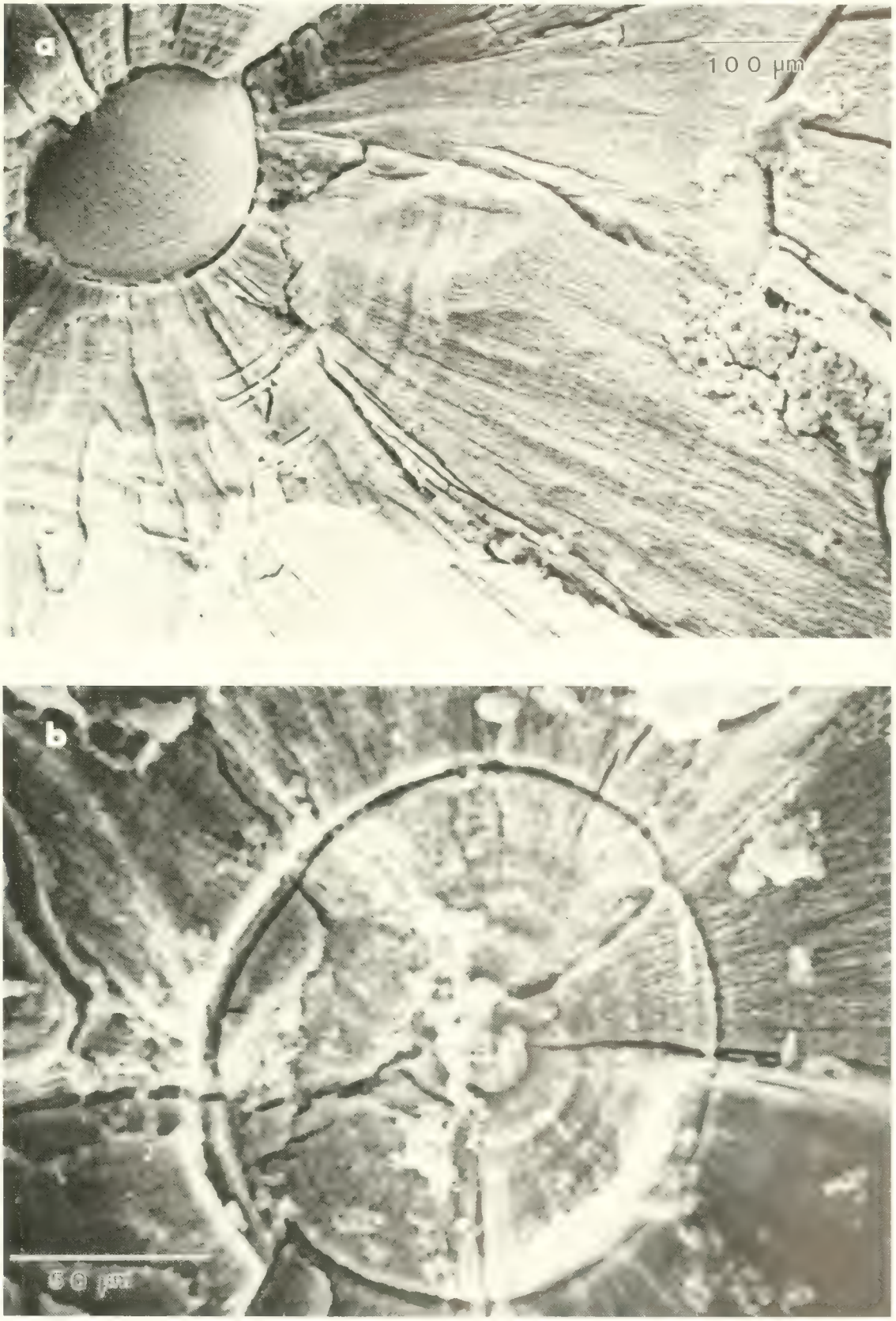
Microincrements were counted in the sagittal otoliths of 32 fishes. Ages ranged from 1.3 years for the small juveniles collected by hand, to 8.5 years for the largest individual collected. Fish length was related to the number of microincrements in the sagitta (Fig. 10). Length (mm) increased linearly with age (years), and was best described by the equation:

$$\mathrm{SL} = 14.87(\mathrm{Age}) + 23.56; (R^2 = 0.93, p<0.0001)$$

No difference in growth was observed between the sexes in our sample (Fig. 10). When separate regressions were calculated for males ($N = 11$) and females

Figure 7

(a) Scanning electron micrograph of a sagittal otolith of a 130-mmSL *Nototheniops nudifrons*, showing the characteristic central core area, or nucleus, separated by a well-defined transitional zone from the outer zone with microincrements radiating outward. (b) Microincrements from a 100-mmSL fish found within the core area of the otolith.


a
100 µm
b
50 µm

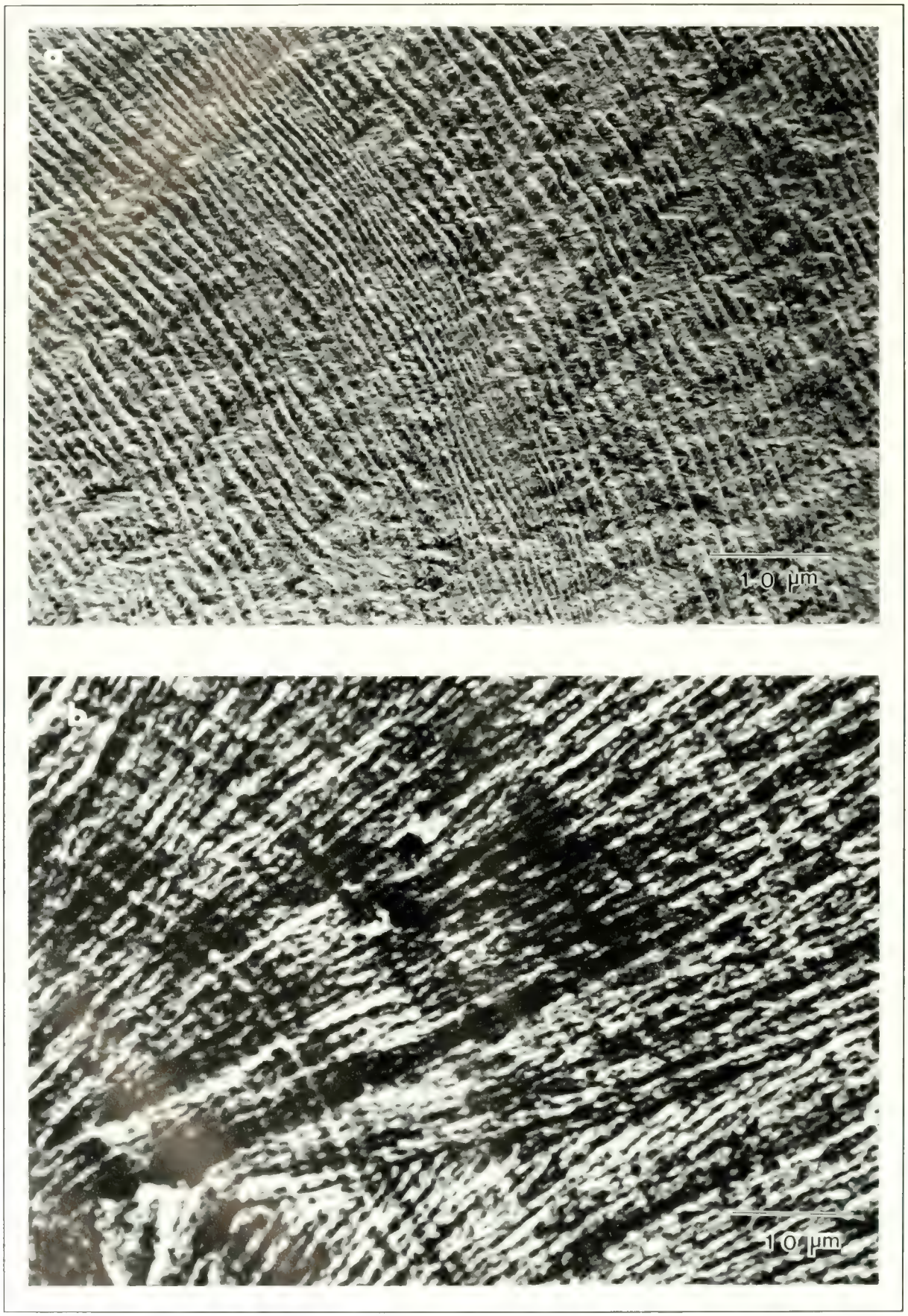

a
1.0 µm
b
1.0 µm

Figure 8

Scanning electron micrographs of microincrements of sagittal otoliths of *Nototheniops nudifrons*, as utilized for daily increment enumeration. (a) Wide and narrow patterns of microincrements from a 144-mmSL fish. (b) Narrow microincrements from a 70-mmSL fish.

($N = 18$), analysis of covariance indicated that the slopes of the two lines did not differ between the sexes (df = 1, 26; $F = 0.82$, $p > 0.37$).

Relationship of fish size and otolith dimensions to fish age

Stepwise multiple regression analysis relating fish size (mm), weight (mg), and otolith morphometrics (sagitta length in mm and weight in μg) to age (years), resulted in the acceptance of the following model:

$$\text{Age (Yrs)} = 3.892 + 0.856(\text{sagitta wt}) - 2.206(\text{sagitta length}) + 0.041(\text{SL}) - 0.025(\text{fish wt})$$

Addition of the remaining variable (sagitta width) did not improve the regression ($N = 32$, $R^2 = 0.967$, $p < 0.05$; Table 3). The residuals were randomly distributed, which demonstrated that this multiple regression best explained the variability in age. Over 94% of the variance was explained by the regression of the two otolith measurements (weight and length). The variables in the model, such as otolith length, width, and weight, are not strictly independent variables, nor are length and body weight. This deviation from the assumptions of the model may result in an artificially inflated R^2 value; however, this should not decrease their practical value as predictors. Sagitta weight alone accounted for 92% of the variance in the regression, supporting the usefulness of otoliths as age-related structures.

The relationship between age and otolith morphometrics allowed the estimation of age for all the fish in the sample (Fig. 11). The growth curve derived from the multivariate model (Fig. 11) was comparable to that derived from microincrement counts (Fig. 10), and both were linear in form. Individuals in this population of *N. nudifrons* grow at approximately 15 mm per year, which is a slow growth rate. Analysis of covariance of

Table 2

Validation of the daily nature of otolith microincrement deposition in *Nototheniops nudifrons*. Otoliths of fish injected with tetracycline were examined by light microscope, while those injected with acetazolamide were examined by scanning electron microscope.

Injection	Number of replicates	Days after injection	Number of post-treatment microincrements counted
Tetracycline	1	4	1
Tetracycline	5	5	2,3,3,3,3
Tetracycline	2	6	3,3
Tetracycline	3	7	4,4,4
Tetracycline	2	9	5,7
Acetazolamide	1	9	4
Tetracycline	5	10	7,7,7,8,10
Tetracycline	1	11	6
Tetracycline	2	14	10,11
Tetracycline	2	15	12,12
Tetracycline	3	16	14,15,16
Acetazolamide	1	21	14
Tetracycline	1	24	23
Tetracycline	2	34	33,34
Acetazolamide	3	158	144,147,149

Regression analysis

	Regression coefficient	SE	t_s	df	p
Tetracycline	b = 1.076	0.074	1.027	27	$0.4 > p > 0.2$
	y-intercept = −3.268	1.036			
Acetazolamide	b = 0.962	0.0049	7.755	3	$p < 0.01$
	y-intercept = −5.402	0.606			

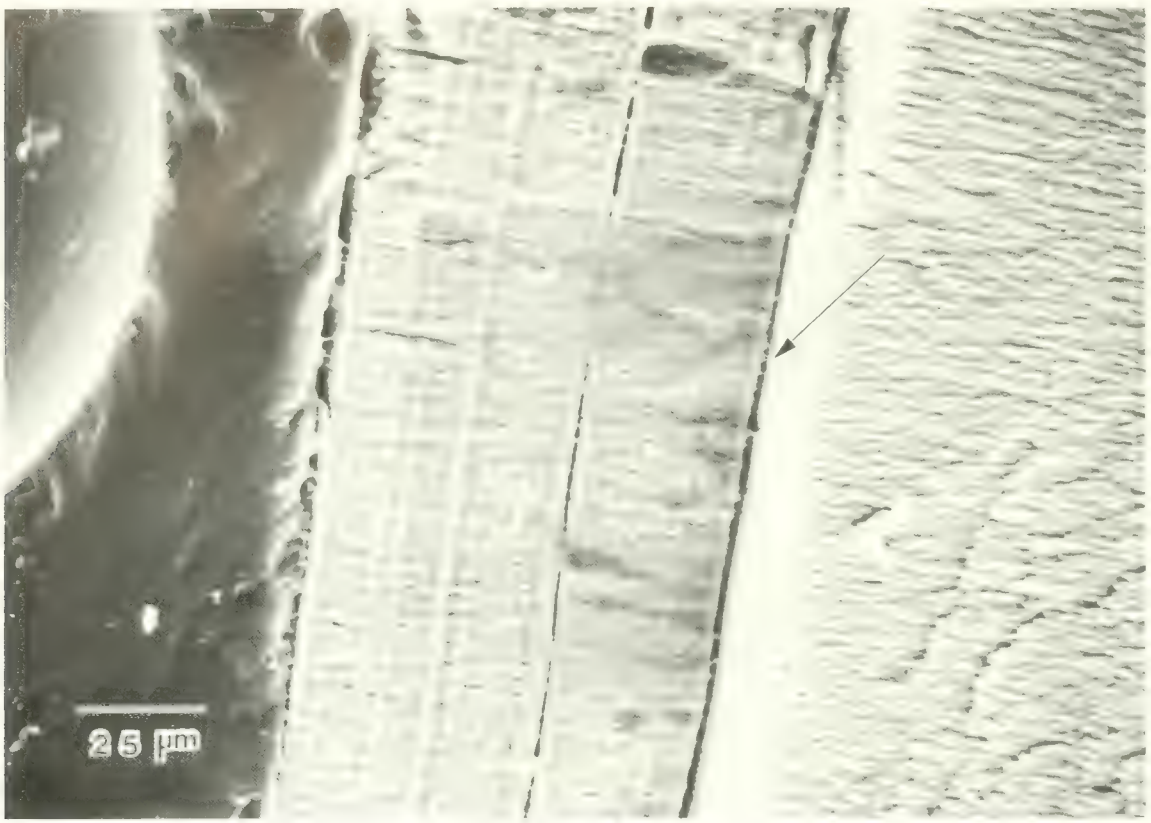


Figure 9

Scanning electron micrograph of a sagitta from a 100-mmSL *Nototheniops nudifrons* marked with acetazolamide. The acetazolamide mark (arrow) is visible as a disruption in the growth increments.

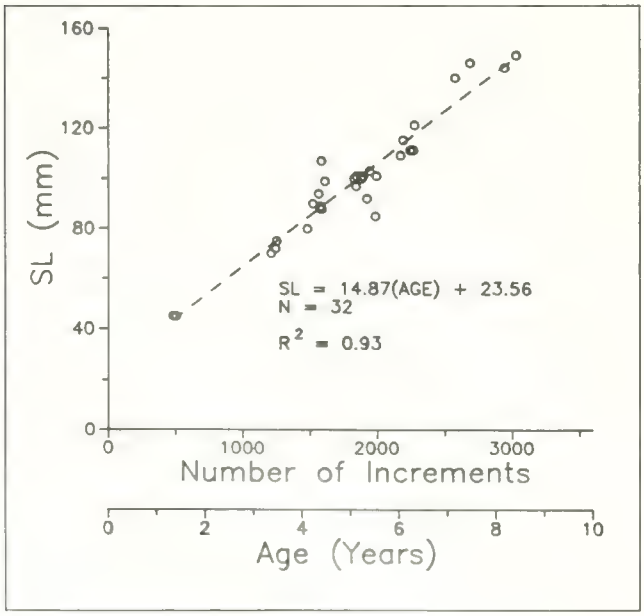


Figure 10

Regression of fish standard length (SL) on age as determined from the number of sagittal otolith microincrements for *Nototheniops nudifrons*.

Table 3

Associated statistics of one-way regression and stepwise multiple-regression model of fish age in years vs. size and weight variables for *Nototheniops nudifrons*. $N = 32$.

One-way regression

	Variable	F	$P>F$	Model R^2
1	Sagitta weight	314.64	0.0001	0.921
2	Fish length (SL)	213.31	0.0001	0.888
3	Fish weight	134.64	0.0001	0.832
4	Sagitta length	103.35	0.0001	0.793
5	Sagitta width	92.43	0.0001	0.774

Multiple regression

Step	Variable entered	F	$P>F$	Partial R	Model R^2
1	Sagitta weight	53.68	0.0001	0.921	0.921
2	Sagitta length	23.16	0.0001	0.021	0.942
3	Fish length (SL)	17.43	0.0003	0.019	0.961
4	Fish weight	4.53	0.0437	0.006	0.967

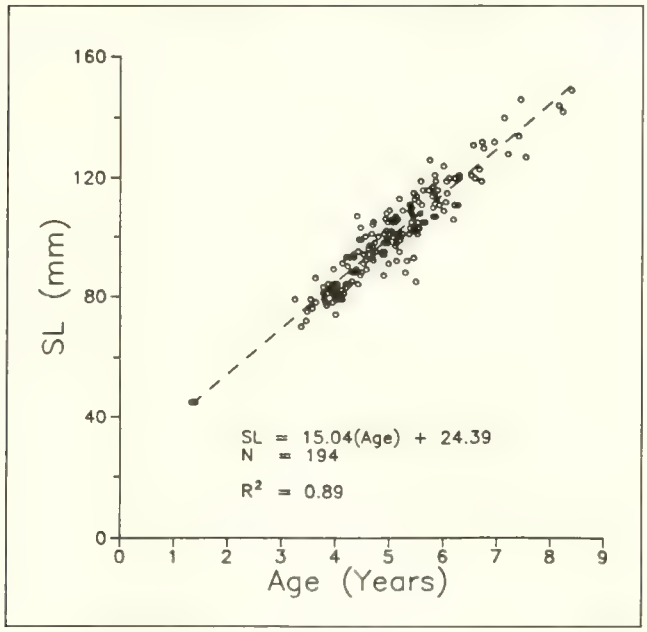


Figure 11
Regression of fish standard length (SL) on estimated age for *Nototheniops nudifrons*. Age was estimated by a multivariate mathematical model based on fish standard length, fish weight, otolith length, and otolith weight.

separate growth curves calculated for males and females showed no significant difference (df = 1,177; $F = 0.87$; $p > 0.36$), indicating that males and females grow at the same rate.

Discussion

Otolith microincrement deposition and age determination

The accuracy of age and growth estimates depends on the assumption that the microincrements viewed were deposited on a daily basis. Daily increments have been found in otoliths from many temperate and tropical fish species (see review by Campana and Neilson 1985). The daily nature of microincrement deposition in *Nototheniops nudifrons* was validated through the tetracycline and acetazolamide marking experiments. Daily increment deposition occurred even during the shortest days of the Antarctic winter. The formation of microincrements may become less regular in some fishes after sexual maturity (Pannella 1980), but our validation study included both immature subadults and mature males and females, which all deposited daily microincrements. Hourigan and Radtke (1989) found that daily microincrement deposition also occurs in larval *N. nudifrons*, beginning at or around the date of hatching. Together, these studies provide the first validation of daily otolith microincrements for any Antarctic fish.

In addition to the microincrements, the otoliths of *N. nudifrons* contained larger banding patterns. In temperate regions, environmental factors such as temperature and food availability show regular and marked seasonal changes, giving rise to clearly identifiable growth periods in fish otoliths. The regular annual formation of these seasonal rings in the otoliths of temperate fishes provides a successful and widely used ageing technique. Growth increments laid down in the otoliths of some Antarctic fishes may be annuli (e.g., *Harpagifer bispinis antarcticus*; Daniels 1983); however, those observed in this study, as well as those in the otoliths of *Nototheniops larseni* (Radtke and Targett 1984), are not. Nevertheless, such increments have been used, perhaps erroneously, for ageing purposes. Compared with temperate zones, Antarctic habitats undergo smaller fluctuations in temperature, which may result in a lack of distinct annual growth increments.

Daily microincrements allow the ageing of Antarctic species without otolith annuli. Microincrements are the result of a discontinuous zone which is generally formed under changing light conditions, probably at daybreak (Tanaka et al. 1981). The near-constant light and constant dark conditions experienced by Antarctic fishes during the summer and winter, respectively, could potentially interfere with daily deposition patterns. However, in the present study, daily increment formation continued despite great variation in photoperiod. Although areas in otoliths were detected in which increment width decreased (Fig. 8), none of these appeared to indicate a cessation of increment formation. Slight changes in light intensity, which occur in both Antarctic summer and winter, or endogenous rhythms may be responsible for the daily pattern of otolith deposition. This problem is currently being investigated using Antarctic fishes kept in constant dark or constant light, and under different light intensities (Radtke and Hourigan unpubl. data).

Use of a multivariate mathematical model relating age to otolith length and weight and fish size is a simpler method of age determination. The preparation and counting of microincrements in fish over 1 year of age is time-consuming and impractical. However, the multiple regression equation calculated from the 32 individuals analyzed with SEM provided an alternative ageing method. Otolith weight (with its consistent relationship to body length) was the best predictor of age, demonstrating the usefulness of otoliths in such a regression. This method should be applicable to other fish species, serving as a quick means to provide growth information. The dimensions of otoliths have been used to estimate the age of temperate fishes (Templeman

and Squires 1956, Boehlert 1985, Radtke et al. 1985). Otolith-age equations are species-specific and possibly population-specific. Using otolith morphometrics for ageing will, therefore, require developing the equations for individual species. Nevertheless, in conjunction with ageing techniques using microincrement counts, otolith morphometrics offer a simpler method of ageing a large sample of individuals than is possible using more laborious techniques.

The external features of *N. nudifrons* otoliths were distinctive compared with those from eight other Antarctic fishes examined (*Chaenocephalus aceratus*, *Champsocephalus gunnari*, *Harpagifer bispinis antarcticus*, *Notothenia angustifrons*, *N. gibberifrons*, *N. larseni*, *N. corriceps*, and *Trematomus newnesi*; Radtke, pers. observ.). Species-specific otolith features of Antarctic fishes have been described by Hecht (1987) and these may be useful in identifying Antarctic fishes from cetacean, pinniped, bird, or fish stomachs (Hecht 1987, North et al. 1984). Otolith morphological characteristics may also provide information on taxonomic relationships among Antarctic fishes (Hecht 1987), as they have for other fish groups (Hecht 1978, Hecht and Hecht 1978, Morrow 1979).

Life history of *Notothenia nudifrons*

Notothenia nudifrons is a slow-growing, relatively long-lived fish. Subadults and adults of both sexes were found in shallow-water (<100 m) benthic habitats along the Antarctic Peninsula, as reported by other researchers (Targett 1981, Daniels and Lipps 1978, Kellermann 1986). The absence of individuals smaller than 75 mm SL from trawls probably represented selection by the fishing gear for larger individuals. The growth curves determined by body length vs. microincrement count, as well as by body length vs. age calculated from the multivariate relations of otolith length and weight, were similar and linear in shape between 45 and 149 mm SL. Linear growth was observed even though the data included a large size-range of fish, with individuals near the largest sizes reported for this species. This type of linear growth, with no marked slowing toward an upper asymptote, has not been reported for other Antarctic fishes, although the growth curve of *Harpagifer bispinis antarcticus*, another small Antarctic fish, is nearly linear (Daniels 1983).

Males and females had similar growth rates. This was surprising, since mature males and females follow different strategies. Males and females reach sexual maturity at the same age (4–5 years); however, thereafter females invest much more energy into gonadal growth than do males (Hourigan and Radtke 1989). All parental care is provided by the males, which may spend at least 4 months in nest defense of a single clutch of eggs (Hourigan and Radtke 1989). This probably requires increased energy costs, and may limit food intake by constraining the male to foraging near the nest. These two strategies may entail similar energy expenditures, resulting in similar somatic growth rates.

Estimation of mortality rates is central to the determination of demographic parameters (Gulland 1955). It is possible to estimate natural mortality (Z) from the data on trawl catches and age for this population of *N. nudifrons*. The most widely used method to estimate mortality is the Beverton and Holt mortality estimator which uses the von Bertalanffy growth curve (Beverton and Holt 1956). The age-length data for the 32 fish were fitted to the von Bertalanffy growth curve, and the parameters and their confidence limits are given in Table 4. These values are primarily useful for comparative purposes, since the actual shape of the growth curve approximated a linear relationship. Natural mortality, calculated from the von Bertalanffy parameters and derived from the sample of 32 fish of known ages, yielded a value of $Z = 0.68$ (Table 4). When Z was calculated using the von Bertalanffy growth parameters for the larger sample of 212 fish with predicted ages, $Z = 0.66$. These estimates assume that the fish grow according to a deterministic von Bertalanffy growth curve. Since the present sample was more accurately represented by a linear growth curve, this assumption was violated. An independent mortality rate was calculated using the actual age estimates from the otolith morphometrics. In this estimate, the mortality rate is the slope of the log-survivorship curve (Ricker 1975) and was calculated to be 0.89.

Kock et al. (1985) provide a summary of mortality estimates for larger Antarctic fishes of commercial interest. Both estimates of instantaneous mortality of *N. nudifrons* were higher than these estimates, which ranged from 0.20 to 0.35. Predation rates may be higher on *N. nudifrons* than on larger species. However, Daniels (1983) estimated the mortality of the still smaller *Harpagifer bispinis antarcticus* to be 0.22 and 0.25 for males and females, respectively (a recalculation of his data for both sexes combined, using the same methods as for *N. nudifrons*, resulted in a value of 0.223).

Although the high mortality rates for *N. nudifrons* accurately describe our sample, they may be subject to sampling errors. Our estimates were based on a single sample captured on two occasions 1 month apart. Both mortality calculations assume that the sampled population is age-stationary (i.e., the age distribution remains the same from year to year), an assumption which is frequently not met. Mortality estimates will also be biased if certain age classes larger than L_C (length at first capture) are less subject to capture. Our

Table 4

Parameter estimates derived from the Von Bertalanffy growth equation (L_∞ constrained to 160 mm SL), natural mortality rates, and associated parameters for *Nototheniops nudifrons* collected from the Antarctic Peninsula.

	SL vs. age in days		SL vs. age in years	
Parameter	Estimate	Confidence limits	Estimate	Confidence limits
From otoliths (N = 32)				
K	0.0005	0.00049–0.00061	0.200	0.000–0.223
t_0	2.20	−158.10–162.50	0.006	−0.434–0.445
From predicted ages (N = 194)				
K	0.00048	0.00047–0.00050	0.175	0.172–0.183
t_0	−40.848	−94.681–12.986	0.112	−0.259–0.036
Mortality estimates (Beverton and Holt 1956)				
	All	Male	Female	
L_r	101	91	101	
L_{Mean}	113.1	106.6	112.5	
k	0.175	0.175	0.175	
Z	0.678	0.599	0.73	
From estimated ages where the mortality rate Z is the slope of the log-survivorship curve (Ricker 1975)				
Z	0.894	0.807	1.26	

sampling caught significantly more females than males (χ^2, $p<0.05$), and the modal size of males was smaller. This might mean that there are fewer large males in this population. Alternatively, larger males may be less subject to capture in spring, perhaps because of different habitat preferences of nesting males. This would skew mortality estimates upwards.

The life history of *N. nudifrons* is characterized by slow growth and a relatively long life for a small fish. Age at sexual maturity is late (4–5 years), and fecundity is low (Hourigan and Radtke 1989). Eggs take several months to hatch, followed by a pelagic larval stage of several months duration (Kellermann 1986, Hourigan and Radtke 1989). It has become clear that these life-history traits are the norm for Antarctic fishes (Daniels 1983, Kock et al. 1985). They combine to produce species that are vulnerable to overfishing and that recover slowly when stocks are depleted. Indeed, catches of both *Notothenia rossii* and *N. gibberifrons* on the shelves of certain islands of the Scotia Sea decreased drastically after several years of fishing (Kock et al. 1985). The methods used in the present study may provide more accurate estimates of the ages of Antarctic fishes, and facilitate management of Antarctic fisheries.

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Abstract. – A study was conducted on shallow banks near Lee Stocking Island, Bahamas, to determine habitat associations of queen conch *Strombus gigas* L. within seagrass meadows of *Thalassia testudinum*. Transect data showed that conch density and biomass increased directly with increasing macrophyte cover up to an optimal level of moderate-density seagrass (608–864 shoots/m^2), after which conch density decreased sharply. Up to the optimal level, conch density and biomass were closely correlated with seagrass and detritus biomass, shoot density, and depth. Seagrass shoot density was the best predictor of conch abundance. Results of habitat choice experiments showed that two different juvenile size classes (75–100 mm and 125–150 mm shell length) are proficient in detecting and choosing habitats with moderate seagrass density over bare sand, low or high seagrass density. Larger conch appear to prefer habitat with higher shoot density than conch of smaller size classes; adult conch were less specialized in their habitat association. These results provide data on one of the key environmental variables, seagrass structure, which will be useful in predicting conch distributions in the field and for planning conch outplanting.

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Distribution and Behavior of Queen Conch *Strombus gigas* Relative to Seagrass Standing Crop

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Seagrass meadows, common in protected shallow waters, are known to be important sources of food and shelter for numerous fishes and invertebrates from high to low latitudes (Kikuchi 1980, Ogden 1980, Virnstein et al. 1984). Living seagrasses are consumed by a few animals such as surgeonfishes, halfbeaks, parrotfishes (Randall 1964, Ogden 1980), urchins (Lawrence 1975), green sea turtles (Ogden 1980), and sirenia (Bertram and Bertram 1968); however, most nonpredaceous fauna of seagrass meadows consume seagrass epiphytes or detritus (Zimmerman et al. 1979, Leber 1983, Fry 1984, Howard 1984, Kitting et al. 1984, Van Montfrans et al. 1984). Sheltering from predation has been shown experimentally for many seagrass inhabitants, particularly crustaceans (Nelson 1979, 1981; Heck and Thoman 1981; Coen et al. 1981; Stoner 1982; Leber 1985; Wilson et al. 1987).

The queen conch *Strombus gigas* L. is a large gastropod mollusc which derives both food and shelter from seagrass beds of the Caribbean region (Bermuda and southeastern Florida to Brazil). After the first year of life, of which little is known, queen conch juveniles emerge from the sediment and feed epibenthically in seagrass meadows where there are large quantities of algal and detrital foods (Randall 1964). Juvenile queen conch are important grazers of seagrass detritus, and conch densities may be limited by food abundance (Stoner 1989). Recent experiments conducted in the Bahamas have shown that seagrasses reduce predation rates on juvenile conch in nursery areas (Marshall and Lipcius, In review).

Throughout its geographic range, the queen conch is an important commercial species which has been severely depleted in many areas (Adams 1970, Brownell et al. 1977). For this reason, there is increasing interest in improving the management of conch, and seeding of depleted areas with hatchery-reared juveniles has been proposed (Berg 1976, Brownell and Stevely 1981, Laughlin and Weil 1983, Coulston et al. 1987). Successful management of the fishery and/or outplanted populations will require detailed information on the relationships between queen conch and environmental variables. This study was conducted to examine the role of macrophyte cover in the distribution of juvenile conch in two nursery areas of the Exuma Cays, Bahamas. In addition to seagrass shoot density and biomass, abundance of detritus, sediment characteristics, and depth were considered for their potential influence on the density, distribution, and biomass of conch. Field experiments were conducted to determine the role of habitat selection in natural conch distributions.

Table 1

Habitat characteristics of the two seagrass meadow study sites. Units for each are: depth (meters at low water), sediment grain size (Ø), organics (% dry wt), *Thalassia shoots* (n/m^2), *Thalassia* and detritus biomass (g dry wt/m^2). Values are means ± SD. n = number of measurements from three transects.

	Stations						
	1	2	3	4	5	6	7
Children's Bay Cay							
Depth (n = 3)	1.0±0.1	1.2±0.1	1.8±0.2	2.7±0.3	3.4±0.3	–	–
Sediment grain size (n = 3)	1.50±0.11	1.38±0.31	1.50±0.07	1.83±0.59	2.44±0.51	–	–
Organics (n = 3)	2.44±0.20	2.35±0.25	2.61±0.06	2.98±0.44	3.88±0.45	–	–
July							
Thalassia shoots (n = 6)	0.0±0.0	64.0±16.0	304±48.0	576±48.0	704±80.0	–	–
Thalassia biomass (n = 6)	0.0±0.0	3.5±1.1	16.0±4.7	48.0±4.8	65.6±14.4	–	–
Detritus (n = 6)	0.0±0.0	0.80±0.80	3.68±1.9	30.9±18.6	104±44.8	–	–
February							
Thalassia shoots (n = 6)	0.0±0.0	67.2±19.2	304±72.0	736±208	864±160	–	–
Thalassia biomass (n = 6)	0.0±0.0	8.6±9.9	13.9±4.6	56.0±20.8	80.0±19.2	–	–
Detritus (n = 6)	0.0±0.0	0.64±0.80	0.64±1.28	48.0±36.8	125±96.0	–	–
Shark Rock							
Depth (n = 3)	1.6±0.1	1.7±0	2.0±0	2.5±0.1	2.8±0.1	3.3±0.3	3.2±0.1
Sediment grain size (n = 3)	1.58±0.06	1.68±0.21	1.96±0.18	2.00±0.13	2.20±0.35	2.57±0.01	2.53±0.10
Organics (n = 3)	2.44±0.03	2.33±0.22	2.34±0.12	2.70±0.11	3.21±0.22	3.57±0.46	2.85±0.47
July							
Thalassia shoots (n = 6)	0.0±0.0	72.0±12.8	256±44.8	528±46.4	669±56.0	741±88.0	728±123
Thalassia biomass (n = 6)	0.0±0.0	5.28±1.4	20.3±4.6	54.4±8.0	62.4±14.4	83.2±1.6	97.6±20.8
Detritus (n = 6)	0.0±0.0	0.48±0.64	3.2±2.7	13.8±13.1	64.0±22.4	96.0±40.0	176±41.6
February							
Thalassia shoots (n = 6)	0.0±0.0	68.8±19.2	292±81.6	452±54.4	608±101	816±217	764±128
Thalassia biomass (n = 6)	0.0±0.0	6.9±4.8	36.8±17.6	68.8±33.6	78.4±14.4	80.0±9.6	115±36.8
Detritus (n = 6)	0.0±0.0	8.0±1.1	1.3±1.9	14.7±15.4	157±35.2	84.8±4.8	309±174

Site description

This study was conducted in the Exuma Cays, Bahamas, at two sites characterized by turtlegrass *Thalassia testudinum* König and known juvenile queen conch populations (Wicklund et al. 1988). The first site (CBC) was located 1.5 km west of Children's Bay Cay (23° 44.3′N, 76°04.5′W). The second site (SR) was located just southwest of Shark Rock (23°45.0′N, 76°07.5′W), a rock outcrop off the southern end of Norman's Pond Cay. There is a gradient in depth at both sites from a shallow sand bar (<1.0 m) to a depth of approximately 3.5 m, accompanied by a gradient in seagrass and detritus biomass (Table 1). Tidal range in the area is approximately 1 m and both sites are subject to strong reversing tidal currents, sometimes exceeding 50 cm/second.

Conch density was highest (~2.0/m^2), near the population centers, decreasing in density towards their peripheries. At each site three transects were made, each separated by approximately 50 m. Divers were towed by a small boat around each site to place buoys on the edges of each population. Transects were then positioned through the population centers, parallel to the depth gradient. Transect lengths were an average of 61 m at CBC and 142 m at SR. Stations marked by stakes were placed along each transect (5 for CBC and 7 for SR) from bare sand to the highest density seagrass. *Thalassia* shoot density was used to set all stations of equivalent number in similar habitats for both sites. Station 1 of each transect was placed on bare sand, with no seagrass or detritus. Stations 2, 3, 4, and 5 were placed in the following approximate shoot densities, respectively: 70, 300, 550, and 700 shoots/m^2. Stations 6 and 7 at SR were characterized primarily by increasing accumulated detritus and higher seagrass biomass and not increasing shoot density.

Methods and materials

Field measurements

Counts were made in July 1988 and February 1989 to test for seasonal differences in conch distribution. In February at CBC we found that the center of the population had moved north of its July location, and

so transect 1 (the southernmost transect) was moved between transects 2 and 3 for the February sampling. Measurements, including station depth, conch density and shell lengths, macrophyte shoot density and biomass, and amount of macroscopic detritus, were taken at each station along the transects within a circle of 2.5 m radius around each stake. Sediment grain-size and organic content were measured in July 1988.

Depths were measured at low water using an electronic depth sounder on a 17-foot Boston Whaler, adjusting for the depth of the transducer below the surface. Using scuba, conch were gathered within each 2.5-m circle at each station, counted, and measured for shell length using large calipers.

A separate collection of 80 conch ranging from 17 to 196 mm in siphonal length was made to generate a length-weight curve. After freezing, the conch were extracted from their shells, washed to remove feces, blotted to remove excess water, and weighed. The following equation describes the significant correlation ($r^2 = 0.987$, $F = 5233.4$, $p < 0.001$) between shell length and wet weight:

$$\log_{10}(\text{wet weight}) = 3.403 \times \log_{10}(\text{length}) - 5.569$$

The equation was used to convert length-frequency data to biomass values.

Two replicate samples of macrophytes and macroscopic detritus (mostly senescent seagrass blades and debris) were collected at each station by haphazardly placing a quadrat with 25-cm sides within each circle. The number of shoots within the quadrat were counted and then collected along with the macrophyte detritus into nylon bags (3.0-mm mesh). *Thalassia* blades (using only aboveground parts), and macrodetritus were separated in the laboratory and dried at 80°C for approximately 24 hours to constant weight. Dry-weight biomass was determined for the individual components.

A core of 40 mm diameter, with a penetration depth of 5 cm, was taken for determination of sediment grain-size distribution and organic content. A subsample of approximately 100 g wet weight was dried at 80°C to constant mass and incinerated at 550°C for 4 hours to determine sediment organic content. Organic content was quantified as the percent difference between dry weight and ash-free dry weight. Another sediment subsample of approximately 50 g was used to determine sediment grain-size. After washing to remove salts and to extract the silt-clay fraction, sand-sized particles were analyzed using standard Ro-Tap procedures. Silt-clay fractions were analyzed using standard pipet procedures (Folk 1966). Product moment statistics were generated for mean grain size and sortedness (McBride 1971).

Habitat preference experiments

Experimental manipulations of plots of seagrasses were made at the Shark Rock site to test for habitat preference in conch of various size classes. Cages 3.6 m diameter (10.2 m^2) were constructed of black plastic mesh with 20-mm openings. The cages were 25 cm high and supported by 1-m long pieces of reinforcement bar driven into the sediment. The bottom edge of the screen was pushed into the sediment approximately 3 cm to prevent escape of conch. No losses occurred during the experiments.

Four cages were built in locations similar to station 5 (see above), characterized by *Thalassia* shoot densities of 700 shoots/m^2 (Moderate Density). Two cages were built near stations 3 with approximately 300 shoots/m^2 (Low Density), and two cages were built in high biomass habitats similar to station 7 with approximately 750 shoots/m^2 plus a heavy layer of detritus (High Density). Macrophytes in two of the moderate-density cages were manipulated so that one-half of each was reduced to 300 shoots/m^2 (Low Density) (Table 2). This was accomplished by placing a rope across the cage through the center and parallel to the direction of flood tide current. (Manipulations were oriented with the current because juvenile conch at the study site are known to move either up or down current during migration.) Then shoots were systematically pulled from one-half of the cage to achieve the desired shoot density. The two cages for this Moderate/Low treatment were manipulated to provide mirror images of one another. The other two moderate-density plots were manipulated in a similar fashion to provide Moderate/Sand treatments, where all seagrass shoots were removed from one side of each cage. Replicate Low/Sand treatments were constructed by manipulating the two low-density plots. High/Moderate treatments were set up by manipulating the high-density plots. About 80% of the loose detritus (comprised mostly of senescent seagrass blades) was removed from half of the high-density plots. Final shoot densities in the high- and moderate-density areas were similar (656 and 672 shoots/m^2, respectively), and removal of detritus yielded a macrophyte environment similar to the moderate-density areas (Table 2). The manipulations required maintenance such as removing new growth and accumulated detritus. Except for the removal of detritus which accumulated along the edges of the cages, maintenance of the plots was performed between the short habitat preference runs.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 2

Summary of biological conditions presented in experiments of habitat preference in queen conch. There were no significant differences between plots in any of the four treatment levels (ANOVA, $p>0.05$).

Treatment	n	Seagrass shoots (n/m^2)	Seagrass biomass (g dry wt/m^2)	Detritus (g dry wt/m^2
Sand	8	0±0	0±0	0±0
Low Density	8	272±32	27±13	3.0±3.5
Moderate Density	12	672±80	72±20	58±37
High Density	4	656±64	98±11	269±66

Between 27 September and 28 October 1988 three conch size-classes were tested for their preferences for habitat type. The classes included animals between 75 and 100 mm shell length (~1 year old), conch between 125 and 150 mm (2 and 3 years old), and adults with the fully developed flare of the shell lip (~4 years or more). All were collected from the seagrass beds around the experimental enclosures. To provide a conch density similar to that in nature, 10 juveniles of a size-class were added to each enclosure (1.0 conch/m^2) after removal of all large invertebrates such as urchins, hermit crabs, and conch. For runs with the adults, 8 animals were placed in an enclosure.

Preliminary experiments showed that the distribution of conch in both Moderate/Low and Moderate/Sand treatments did not change significantly between 1 and 5 days; therefore, all runs were terminated at 3 days. At the end of a run, the numbers of conch found on each side of the cage were recorded, and the animals were removed. Because the animals touching the screen may have been moving around the periphery of the enclosure, they were not included in the counts. Three or four runs were made for each size-class and treatment, except those in the High/Moderate enclosures where two runs were made in each cage. No significant differences were found in the distribution of animals in a size-class in any of the pairs of cages providing similar combinations of macrophytes (Fisher's Exact Test, $p>0.05$); therefore, the paired cages were considered to be replicates.

Results

Station characteristics

Average depths for the five stations at CBC increased from station 1 (1.0 m) to station 5 (3.4 m). Average station depths for SR increased from station 1 (1.6 m) to station 6 (3.3 m) and then decreased slightly at station 7 (3.2 m). *Thalassia* shoot density, biomass, and detritus biomass all increased with increasing station number and depth, with a few exceptions (see Table 1). At CBC shoot density ranged from 0.0 to 864 shoots/m^2, *Thalassia* biomass from 0.0 to 80 g dry wt/m^2, and detritus biomass from 0.0 to 125 g dry wt/m^2. At SR shoot density ranged from 0.0 to 765 shoots/m^2, *Thalassia* biomass from 0.0 to 115 g dry wt/m^2, and detritus biomass from 0.0 to 309 g dry wt/m^2.

Sediment grain-size at the CBC transects was relatively constant (1.38–1.83 Ø) between stations 1 and 4, but finer at station 5 (2.44 Ø). Sediment organic content increased slightly over the transects from low-biomass to high-biomass stations. At the SR transects mean grain diameter decreased (increasing Ø) from stations 1–6, while stations 6 and 7 had nearly equal grain size (2.57 and 2.53 Ø). Organic content was highest at SR station 6, but values ranged only from 2.33 to 3.50% of dry sediment weight.

Children's Bay Cay and the Shark Rock site showed highly significant correlations among all of the variables: water depth, seagrass shoot density, aboveground seagrass biomass, and standing crop of macrodetritus (Table 3). Weakest correlations ($r = 0.586$ to 0.631) occurred between detritus and the other variables at Shark Rock in February, when abundance of detritus was low. Correlations between macrophyte and depth characteristics remained highly significant when all sites, stations, and dates were included in regression models (Table 3) suggesting that the relationships are relatively universal in the study area. The highest correlation occurred between seagrass shoot density and water depth ($r = 0.930$), and weakest correlations were found between detritus biomass and the other variables.

Conch density patterns

At CBC there was an increase in conch density in both July and February along the transects from station 1–5, except for a small decrease in February from station 4 to station 5 (Fig. 1). Densities in July were similar

Table 3

Pearson correlation matrices showing the relationships among depth and macrophyte variables at the seagrass meadow study sites. The upper and lower sections of the first two matrices are for July and February collections, respectively. The bottom matrix is for all stations and dates combined. Shoots = density of *T. testudinum* shoots; *Thalassia* = biomass of *T. testudinum*; Detritus = biomass of macrodetritus.

	Depth	Shoots	*Thalassia*	Detritus
		Children's Bay Cay		
Depth	–	0.966**	0.938**	0.911**
Shoots	0.968**	–	0.961**	0.817**
Thalassia	0.873**	0.880**	–	0.839**
Detritus	0.728**	0.752**	0.826**	–
		Shark Rock		
Depth	–	0.969**	0.964**	0.839**
Shoots	0.950**	–	0.954**	0.769**
Thalassia	0.877**	0.891**	–	0.889**
Detritus	0.631*	0.586*	0.623*	–
		Combined sites and dates		
Depth	–			
Shoots	0.930**	–		
Thalassia	0.871**	0.887**	–	
Detritus	0.648**	0.628**	0.726**	–

* $p<0.05$; ** $p<0.01$.

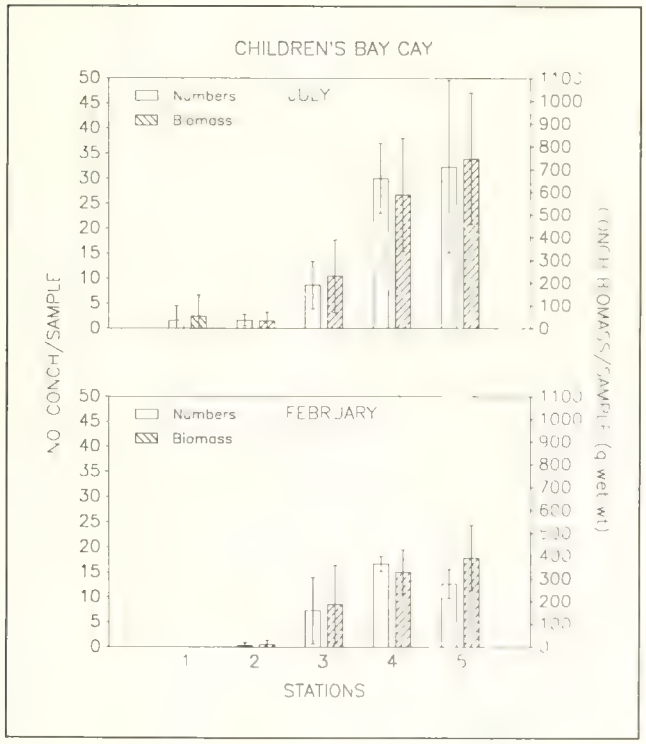

Figure 1

Number of conch and conch biomass sampled within a 2.5-m radius circle at Children's Bay Cay, July 1988 and February 1989, at each station. Values are means ± SD.

to those in February at stations 1, 2, and 3. Stations 4 and 5 had densities almost twice as high in July as those in February. At SR, the general pattern was an increase in conch density from station 1–5 (except a small decrease in July at station 4) (Fig. 2). In July, the density then decreased sharply at stations 6 and 7. In February, the density increased further at station 6 and then decreased at station 7. More pronounced than at CBC, the densities at SR in February at stations 3, 4, and 5 were lower than the July densities.

After log transformation of the data to improve heterogeneity in the variance, a multi-way ANOVA was used to test for differences and interactions in conch density between sites, dates, transects, and stations (Table 4). Transects were examined as blocks, and hence there were no interaction terms with transect. Since SR had 7 stations as opposed to 5 at CBC, stations 6 and 7 at SR were not used in this analysis where CBC and SR were compared.

There were no significant interaction terms or block (transect) effects in the ANOVA ($p>0.05$); therefore, the effects of date, site, and station may be interpreted directly. It is clear from Figures 1 and 2 that conch densities were higher in July than in February at both CBC and SR at most stations. Significant site effects appear to be related to the low numbers of conch at SR, particularly in February and at station 1–3. Station effects occurred because of the increase in conch

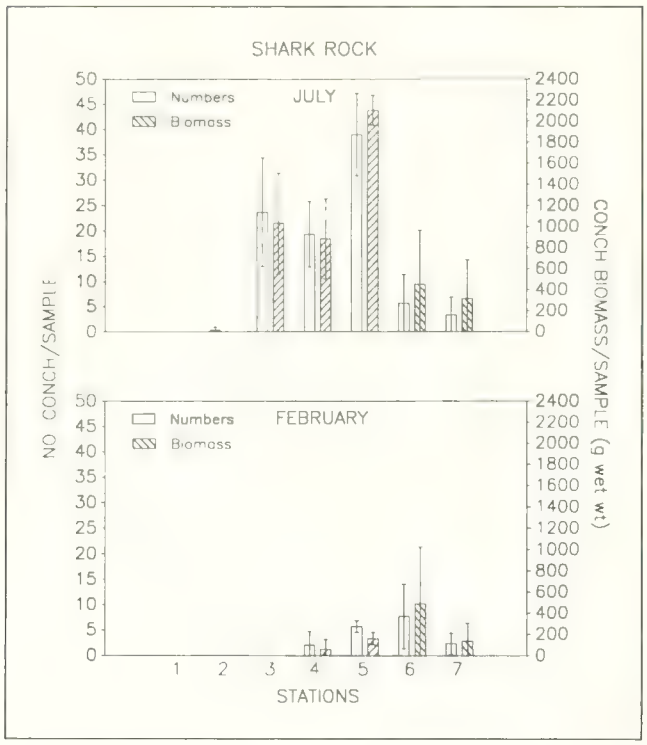

Figure 2

Number of conch and conch biomass sampled within a 2.5 m radius circle at Shark Rock, July 1988 and February 1989, at each station. Values are means ± SD.

Table 4

Results of multi-way analysis of variance for conch density in seagrass meadows. Data were log-transformed and transects were examined as blocks.

Source	df	MS	F	p
Date	1	2.503	22.755	<0.0001
Site	1	0.753	6.846	0.011
Transect	2	0.032	0.289	0.750
Station	6	2.400	21.820	<0.0001
Date * Site	1	1.047	3.058	0.086
Date * Station	6	0.539	1.574	0.171
Site * Station	6	0.160	0.468	0.829
Date * Site * Station	6	0.228	0.642	0.696
Error	56	0.355		

Table 5

Results of multi-way analysis of variance for conch biomass in seagrass meadows. Data were log-transformed and transects were examined as blocks.

Source	df	MS	F	p
Date	1	9.349	15.564	<0.0001
Site	1	3.025	5.036	0.028
Transect	2	0.155	0.258	0.773
Station	6	11.511	19.162	<0.0001
Date * Site	1	3.838	2.372	0.129
Date * Station	6	1.868	1.154	0.343
Site * Station	6	1.614	0.997	0.436
Date * Site * Station	6	1.032	0.610	0.722
Error	56	1.692		

density between stations 1 and 5 at all sites and dates, except SR station 4.

A one-way ANOVA and a Newman-Keuls multiple range test were used to test for differences in log transformations of conch density among stations 1–5 combining all sites and dates (CBC–July, SR–July, CBC–February, SR–February). There was a significant difference between stations ($F = 22.02$, $p<0.0001$). Conch densities increased with increasing station number, ranging from 0.42 (±1.38) to 22.4 (±15.8). Newman-Keuls tests showed that the logs of conch density at stations 1 and 2 were significantly different from all other stations, though not from one another, as were stations 4 and 5. Station 3 was significantly different from all other stations (Newman-Keuls, $p<0.05$).

Conch biomass patterns

As with conch density, there was an increase in conch biomass at CBC, from stations 1 to 5. The pattern was strong for both July and February, although the actual biomass values were higher in July at stations 4 and 5 than in February. At SR the biomass also increased from stations 1 to 5 (with a slight decrease at station 4 in July). In July, biomass decreased sharply at station 6 and 7, while in February the biomass continued to increase at station 6 and decreased at station 7. In July stations 3, 4, and 5 had much higher biomass values than in February.

After log transformations of the biomass data, a multi-way ANOVA was used again to test for differences or interactions between dates, sites, transects, and stations in conch biomass with transects examined as blocks (Table 5). Where CBC and SR were compared, stations 6 and 7 at SR were not used.

There were no significant interaction terms and no block effects on the ANOVA ($p>0.05$), therefore the effects of date, site, and station are interpreted directly. As mentioned above, conch biomass at both CBC and SR was higher in July than in February at most stations. Site differences appear to be due to low biomass values in February at SR, especially at stations 1–3. Station differences clearly resulted from the increase of conch biomass with the increase in station number, at all sites and dates, except SR station 4.

Table 6

Pearson correlation coefficients for relationships between measures of conch abundance and characteristics of seagrass habitat for different months and sites. CBC = Children's Bay Cay site; SR = Shark Rock site. At the Shark Rock site, analyses were made with 5 and 7 stations because of decreasing numbers of conch at stations 6 and 7 (see text).

	CBC	CBC	SR (5 stations)		SR (7 stations)	
	July	Feb.	July	Feb.	July	Feb.
Conch density						
Depth	0.868**	0.868**	0.813**	0.837**	0.168	0.650**
Shoots	0.860**	0.851**	0.831**	0.787**	0.314	0.726**
Thalassia	0.910**	0.753**	0.779**	0.803**	0.141	0.495*
Detritus	0.608*	0.753**	0.701**	0.853**	0.141	0.495*
Conch biomass						
Depth	0.774**	0.892**	0.850**	0.801**	0.216	0.530*
Shoots	0.874**	0.831**	0.863**	0.741**	0.423	0.634**
Thalassia	0.886**	0.781**	0.836**	0.799**	0.270	0.353
Detritus	0.680**	0.597*	0.827**	0.780**	0.004	0.244

Combined sites and dates (5 stations)

	Conch density	Conch biomass
Depth	0.603**	0.492**
Shoots	0.636**	0.513**
Thalassia	0.518**	0.438**
Detritus	0.330*	0.266*

*$p<0.05$; **$p<0.01$.

A one-way ANOVA and a Newman-Keuls multiple range test were used to test for differences in log transformations of conch biomass among stations for all date-site samples. There was a significant difference in the log of conch biomass across stations. Conch biomass increased from 13.4 g wet weight (±44.5) at station 1 to 851 g wet weight (±766) at station 5. The log of conch biomass at stations 1 and 2 were not different from one another but were each significantly different from stations 3, 4, and 5. Stations 3 and 5 were each significantly different from all stations but station 4 (Newman-Keuls, $p<0.05$).

Relationships between conch and the independent variables

There were highly significant correlations between both density and biomass of conch in the field and the depth and macrophyte characteristics of the habitat (Table 6). Tested by individual date at Children's Bay Cay, correlations between conch density and depth, shoot density, and seagrass biomass were high and relatively similar (r values between 0.753 and 0.910), while correlations with detritus were significant but lower. Similar patterns held for conch biomass. At Shark Rock in July, conch numbers and biomass were highest at station 5 (Fig. 2) and did not increase over the entire range of seagrass shoot density or biomass. Therefore, linear regressions of conch density and biomass with depth and macrophyte characteristics did not yield high or significant correlations in most cases when data from all seven stations were included (Table 6). Highly significant correlations were found using the first five stations; all of the habitat characteristics yielded correlation coefficients between 0.701 and 0.863 (Table 6).

In regression models including data from all dates, sites, and stations 1–5, all of the environmental variables yielded significant correlations with conch density and biomass (Table 6). Highest correlations occurred between seagrass shoot density and both conch density and conch biomass. Lowest correlation coefficients occurred with detritus.

Two stepwise multiple regressions were run to determine the best multiple regression models for conch density and conch biomass using all of the data for stations 1–5 (all dates and sites combined). Alpha to enter and remove from the models was set at 0.150. The regression model for conch density included first shoot density followed by detritus standing crop, and yielded a

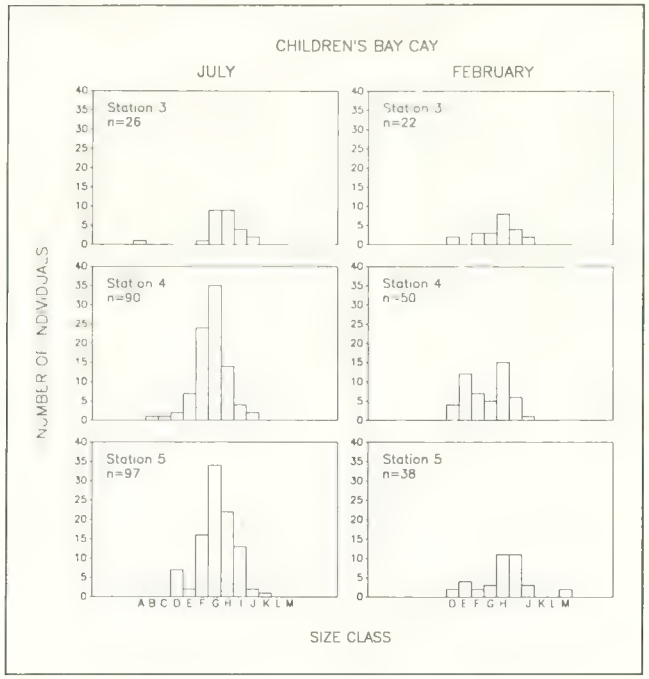

Figure 3

Number of individuals per sample (2.5-m radius circle) within each conch size-class for each station at Children's Bay Cay, July 1988 and February 1989. Size-classes are as follows: A = 40–49 mm, B = 50–59 mm, C = 60–69 mm, D = 70–79 mm, E = 80–89 mm, F = 90–99 mm, G = 100–109 mm, H = 110–119 mm, I = 120–129 mm, J = 130–139 mm, K = 140–149 mm, L = 150–159 mm, M = 160–169 mm, N = 170–179 mm, O = 180–189 mm, P = 190–199 mm, and Q = 200–209 mm.

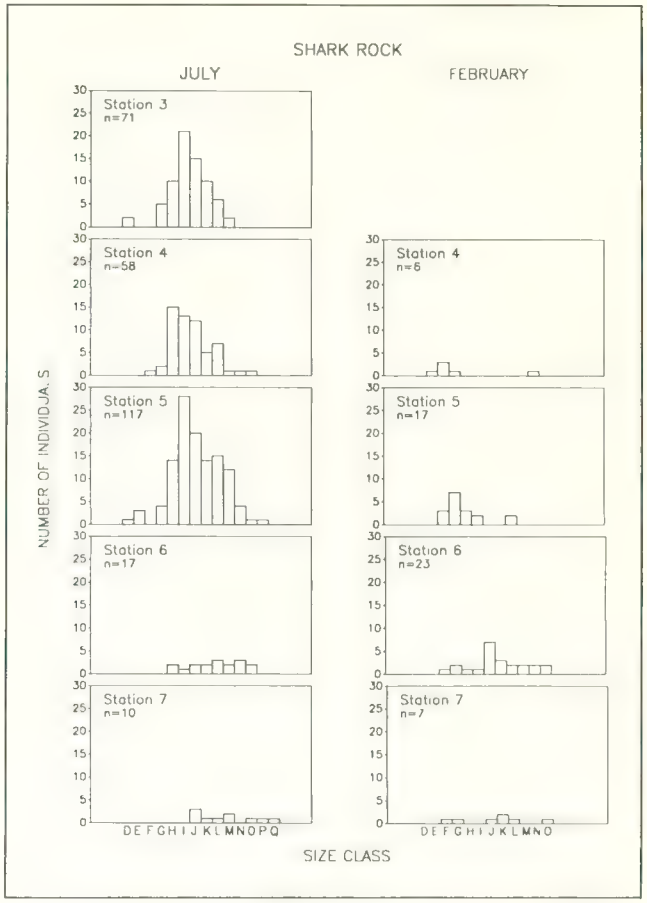

Figure 4

Number of individuals per sample (2.5-m radius circle) within each conch size-class for each station at Shark Rock, July 1988 and February 1989. For size-classes see Figure 3.

multiple correlation coefficient of 0.664 ($p<0.001$). The stepwise multiple regression model for conch biomass included only shoot density and provided a multiple regression coefficient of 0.513 ($p<0.001$). No other variables contributed significantly to the correlation.

Results of the regressions and the Newman-Keuls tests for conch density across stations indicate that stations 3–5 provide a suitable habitat for conch larger than 70 mm SL with habitat characteristics ranging as follows: 256–864 mean shoots/m^2, 13.9–80.6 mean g dry wt of *Thalassia*/m^2, and 0.64–157.12 mean g dry wt of detritus/m^2. In addition, the correlation between conch and macrophyte characteristics are linear only up to station 5 (608–864 mean shoots/m^2, 62.4–80.6 mean g dry wt of *Thalassia*/m^2, 64.0–157.1 mean g dry wt of detritus/m^2) which appears to be the near-optimal habitat for juvenile conch larger than 70 mm.

Conch length-frequency patterns

The Kolmogorov-Smirnov two-sample test was used to test for significant differences in the length-frequency distribution of conch at different stations. Only stations with at least 10 conch were used in the analysis (CBC stations 3–5 in both July and February; SR stations 3–7 in July and stations 5–6 in February).

In July, CBC stations 3, 4, and 5 all had significantly different conch length-frequencies (stations 3 and 4, $p<0.0001$, stations 3 and 5, $p=0.015$, stations 4 and 5, $p<0.0001$). Mean lengths varied only from 102 to 111 mm, and the statistical differences were a result of subtle differences in the shape of the distributions (Fig. 3). In February at CBC, the length-frequency distribution of conch at station 3 was different significantly from that at station 4 ($p=0.004$), and the distribution at station 4 was different significantly from that at station 5 ($p<0.0001$). The length-frequencies at stations 3 and 5 were not different ($p=0.062$); the mean values and shapes of the distribution were similar (Fig. 3).

In July, conch length-frequency patterns at SR stations 3, 4, and 5 were not different (stations 3 and 4, $p=0.220$; stations 4 and 5, $p=0.260$), and had means

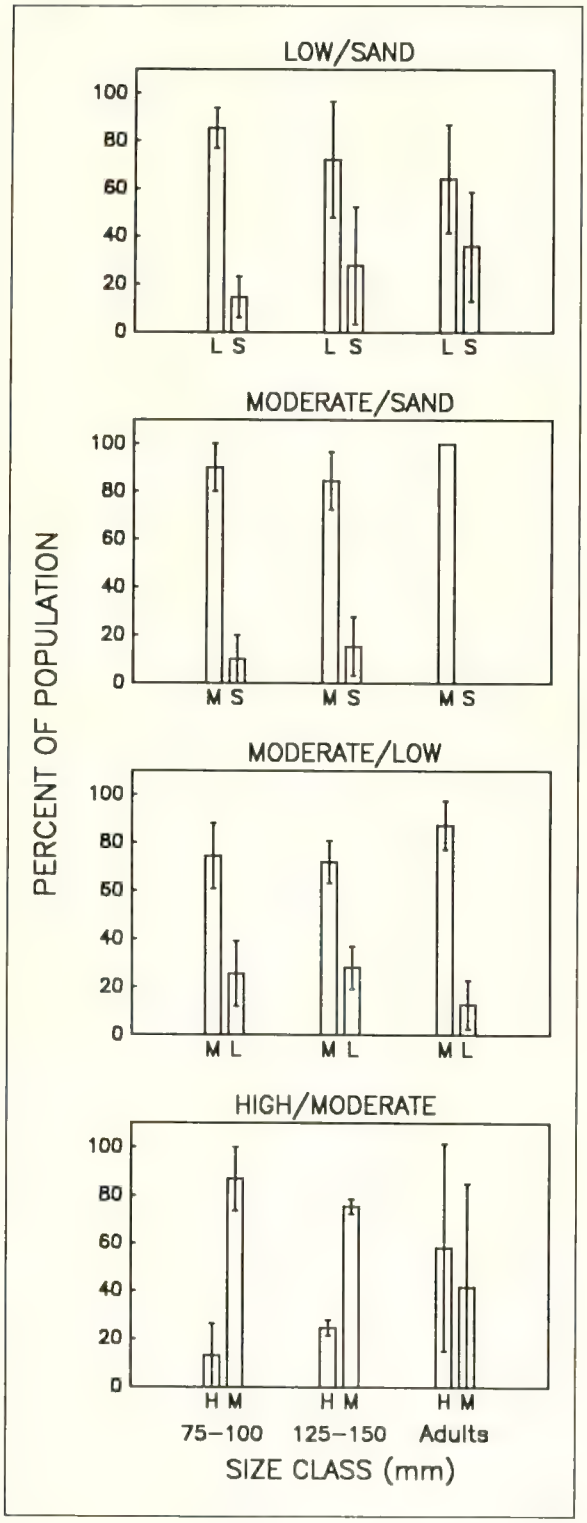

Figure 5

Percentage of conch in three size-classes found within a habitat type from a choice of two types. Choices included combinations of bare sand, low and high seagrass biomass.

Table 7

Results of *G*-tests on habitat choice by three size-classes of conch presented with paired habitats.

Size-class (mm)	No. of runs	Total no. of conch in the habitats	G_{adj}	p
Low/Sand treatments				
75–100	6	37/6	24.86	<0.01
125–150	6	28/9	10.24	<0.01
Adults	6	6/5	0.09	>0.05
Moderate/Sand treatments				
75–100	6	53/7	42.99	<0.01
125–150	8	61/10	36.41	<0.01
Adults	6	33/0		<0.01
Moderate/Low treatments				
75–100	6	44/17	12.27	<0.01
125–150	6	38/22	9.72	<0.01
Adults	6	31/5	20.89	<0.01
High/Moderate treatments				
75–100	4	2/23	20.72	<0.01
125–150	4	8/25	9.19	<0.01
Adults	4	4/3	0.14	>0.05

between 129 and 136 mm. Distributions at stations 6 and 7 were not different ($p = 0.749$) (Fig. 4). This pattern of size-frequency distribution showed that, in July, conch were significantly larger at the stations with higher macrophyte biomass (stations 6 and 7), while smaller conch were found at sites with moderate-to-low seagrass biomass (stations 3, 4, and 5). In February, the two SR stations with more than 10 conch—stations 5 and 6—had significantly different length-frequencies ($p<0.0001$) (Fig. 4). Again, the large conch were associated with high seagrass biomass.

Habitat preference experiments

Results of the habitat preference experiments showed that conch were proficient in detecting and choosing habitats with different macrophyte characteristics (Fig. 5). Of the conch in all size classes, 90% were associated with the moderate density plots as opposed to sand habitat (10%). Habitat selectivity was less strong in the other habitat pairs, but it is clear that plots with seagrass present were selected over bare-sand habitats, and moderate-density seagrass was selected over either high- or low-density seagrass.

Heterogeneity G tests showed that the results of runs within all of the individual habitat preference tests were homogeneous ($p<0.05$) except one (Low vs. Sand; 125–150 mm; $G_H = 14.37$, $p>0.05$). Standard G tests were used with the pooled data to test the null hypothesis that animals were distributed equally over

the two sides of the enclosures. All treatments and size-classes resulted in highly significant differences ($p<0.01$), except for two cases (Table 7). Adults in the Low/Sand treatment and adults in the High/Moderate treatment showed no significant habitat preference ($p>0.05$). In these two experiments adult conch were highly motile, and more than 50% of the individuals were found traveling around the walls of the enclosures. Because only animals not touching the walls were included in the analysis, the numbers for analysis were small and highly variable (Table 7, Fig. 5). Where a high-preference habitat (Moderate Density) was paired with a low-preference habitat (Low Density or Sand), adult conch were not found against the walls of the enclosures in such high numbers (28%) and habitat selection was highly significant (Table 7).

Discussion

Many marine organisms are known to prefer seagrass beds over bare sand. For example, amphipods, tanaidaceans, decapods, and fishes have all been found to be more abundant in seagrass beds than on bare sand (Heck and Thoman 1981, Holt et al. 1983, Stoner 1983, Heck et al. 1989). Also, abundance of animals within seagrass beds appears to be influenced strongly by the local amount of macrophyte structure. Numbers of both decapod and peracarid crustaceans have been correlated with seagrass biomass (Heck and Orth 1980, Stoner 1980a, Lewis 1984). A direct linear relationship between seagrass biomass and harpacticoid abundance and diversity was attributed to an increase in habitable space, nutritional resources, and reduced levels of predation (Hicks 1980). Communities of epibenthic fish on the banks of Florida Bay were associated with areas of high seagrass biomass and with accumulations of seagrass detritus (Sogard et al. 1987). Detritus was thought to provide a rich food source as well as a refuge from predators.

The general association of queen conch with turtlegrass *Thalassia testudinum* is well known (Randall 1964, Hesse 1979, Weil and Laughlin 1984), but quantitative relationships between the mollusc and seagrass beds are reported for the first time in this study. The distributional patterns of queen conch near Lee Stocking Island were similar to patterns found for other taxa, with few individuals associated with bare sand and low-density seagrass. As was true for other species, juvenile conch densities increased with macrophyte biomass and shoot density over a wide range; however, optimal levels of macrophyte cover were found, beyond which only larger individuals were associated. The observed association of juvenile queen conch with moderate amounts of macrophyte cover (shoot density, biomass, etc.) probably results from a combination of mechanisms: (1) a simple inability of the animals to maneuver into or through heavy stands of seagrass and detritus, (2) active habitat choice for specific seagrass cover, and (3) differential survivorship associated with different macrophyte densities, especially in the smaller size-classes.

The upper limit of seagrass density with which juvenile queen conch are associated is probably set by their locomotory abilities. Randall (1964) speculated that thick stands of seagrass obstruct the movements of small conch. High shoot density is also responsible for heavy accumulations of detritus and soft sediments which may impede locomotion. Given that queen conch propel their heavy shells with thrusts of a pointed operculum on the end of a muscular foot, locomotion is most efficient on a firm substratum.

The direct relationship between conch density and seagrass density below the optimal level is most likely linked to more complex interactions. It is known that abundance of food can be limiting for juvenile conch in the field at natural density (Stoner 1989). The primary sources of food for juvenile conch in nursery habitats are macrodetritus and algal epiphytes (Stoner and Waite, In review); both of these food items increase with seagrass density. Blade and detritus productivity increase with shoot density, and seagrasses have the effect of increasing the entrapment of fine sediments and detritus (den Hartog 1967, Orth 1977, this study), useful only up to the point of impeded locomotion. Algae consumed by conch in the seagrass nursery areas are primarily those growing as epiphytes on *Thalassia* blades. Production of these epiphytes can be as high as 50% of the seagrass production (den Hartog 1979), and increases with seagrass shoot density. The increase in density of conch with seagrass shoot density, therefore, may be a function of habitat choice by individuals for areas with greater abundance of foods and/or a function of food limitation in the population.

The relationship between conch density and seagrass shoot density can also be a response to predation. This response could be direct, whereby the survivorship of conch increases with increasing seagrass structure, or indirect, where habitat preference for high-structure habitats has evolved as a response to predators. In either case, the role of seagrass biomass in protecting prey species is known for a wide variety of predator-prey combinations (Coen et al. 1981, Stoner 1982, Leber 1985, Heck and Wilson 1987), and experiments with crustaceans have shown that prey species are proficient in choosing high-density seagrass (Stoner 1980b, Coen et al. 1981, Bell and Westoby 1986). The fact that small conch were more proficient in selecting habitats of particular seagrass biomass or shoot density than

large individuals suggests that there is strong selective pressure for habitat choice in small conch, probably via size-specific mortality. Susceptibilty of juveniles to predation is known to decrease with increasing conch size (Appeldoorn 1984).

Whether the observed distributional patterns are ultimately a response to foods and/or predators cannot be determined from data presented here; however, new experiments using artificial structures and predator manipulations would be useful. In any case, strong habitat preferences suggest that evolved behavioral mechanisms are influential, and the evolution of habitat choice in conch is probably related to both procurring sufficient foods and avoiding predators.

Significant effects of date in the density and biomass of conch in the seagrass beds was related to the normal seasonality of reproduction and recruitment in conch of the Exuma Cays. The 1+ year-class (~40–100 mm), spawned during the previous summer (1987), was most abundant in July. In the Exuma Cays, spawning occurs between April and October (Stoner et al. In review), with greatest recruitment to the benthos probably occurring between August and October. Juvenile conch spend most of their first year buried in the sediment; therefore, only the 1987 and older cohorts were surveyed in July 1988 and February 1989. In February, the 1988 cohort had not yet emerged from the sediment and, therefore, the 1+ year-class was not found in that survey.

Information on the settlement and distribution of juvenile conch in their first year of life will be particularly useful in elucidating mechanisms of distribution and abundance. Conch less than 40 mm have been found in very shallow, unvegetated subtidal sediments, moving to deeper waters or seagrass beds with age (Weil and Laughlin 1984; Stoner and Sandt, unpubl. data). Highest abundance of 1-year-old conch in sparse seagrass close to sand shoals, therefore, could be a result of ontogenetic migration.

The relationship between juvenile conch and easily measured characteristics of the macrophyte community should prove useful in predicting conch distributions and in planning stock-enhancement programs involving the seeding of hatchery-reared conch. The lack of statistical interaction among the factors site, station, and date suggests that the strong relationships between conch and seagrass shoot density (and other macrophyte characteristics) are relatively universal. It must be pointed out, however, that the surveys were conducted within areas known to be long-term conch nursery sites, and there are extensive areas of seagrasses on the Exuma Bank near Lee Stocking Island which appear to have similar habitat characteristics but no resident conch populations. Recent transplant experiments have shown that many of the habitats with appropriate seagrass, sediment, and detritus characteristics do not provide good growth or survivorship in juvenile conch (Stoner and Sandt, In press). Clearly, there are unmeasured variables in the seagrass meadows which are important aspects of habitat quality for conch. Habitats without natural conch populations, which produced good growth and survival rates, may be recruitment limited. Such limitation may be a function of larval supply or ontogenetic movements in the species. This study demonstrates that there is a strong relationship between conch density and biomass and the amount of seagrass structure in the habitat; however, general seagrass characteristics cannot be used as predictors of conch distribution independent of other variables such as food quality, presence of predators, hydrographic considerations, and recruitment processes.

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Key to the Hippolytid Shrimp of the Eastern Pacific Ocean

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Abstract.—Seventy-two species of hippolytid shrimp (Decapoda: Crustacea: Hippolytidae) have been reported from the eastern Pacific (the Aleutians to Cape Horn). There are more species to the north of Magdalena Bay, Baja California, than in tropical or temperate waters to the south. Most species of *Eualus*, *Lebbeus*, *Heptacarpus*, and *Spirontocaris* live along the temperate coasts of North America; species of *Thor*, *Trachycaris*, and *Lysmata* are most common in warm-temperate to tropical areas, and species of *Hippolyte* range from cool to tropical regions. In the eastern Pacific, species of *Nauticaris* and *Leontocaris* have been found only in the Southern Hemisphere. An annotated key to the species, with geographic and depth range and selected synonyms, is provided.

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Members of the family Hippolytidae are among the most abundant and diverse carideans of the eastern Pacific. Hippolytids are eaten by birds and fishes, and serve as cleaners for fishes such as moray eels (Chace 1937, Limbaugh 1961, Hobson and Chess 1976, Reynolds 1977). They are common inhabitants of tidepools, kelp beds, seagrass flats, and other nearshore areas, but also range into the deeper parts of the continental shelf and slope.

The greatest diversity of species of hippolytids in the eastern Pacific is in boreal to temperate waters of the northern hemisphere (Table 1). Forty-seven species live from the Aleutian Islands to Baja California, Mexico. Among these, *Lebbeus vicinus* has the greatest range, from the Aleutians to the Gulf of California. *Hippolyte californiensis* lives from the coast of Alaska to the Gulf of California. Eighteen other species range from the Aleutians or the mainland of Alaska south to southern California, USA, or Baja California, Mexico. Twenty-one species range from the Bering Sea or the Aleutians to British Columbia, Washington, or Oregon. Two species have been reported only from Puget Sound, and four species range from the Bering Sea or the Aleutians to northern or central California. An additional six species range from central California to Baja California or the Gulf of California, Mexico.

In the Northern Hemisphere, species of *Spirontocaris*, *Heptacarpus*, *Eualus*, and *Lebbeus* are diverse. Species of the first two genera are not found in the Southern Hemisphere, while species of the latter are more diverse in the northern than in the southern hemispheres. Although no species of these genera are found off both North and South America, *Lebbeus washingtonianus* and *L. bidentatus*, and *Eualus pusiolus* and *E. dozei* are very similar and may represent pairs of disjunct sibling species.

Tropical areas of the eastern Pacific are poor in hippolytid species. *Lysmata californica* ranges from central California to the Galapagos, while *Latreutes antiborealis* ranges from the Gulf of California to Chile. *Thor algicola* and *L. antiborealis* are sibling species of *T. manningi* and *L. parvulus* of the Caribbean and warm-temperate western Atlantic. *Hippolyte zostericola*, *Trachycaris restrictus*, and *Lysmata intermedia* occur both in the eastern Pacific and in the Caribbean and tropical Atlantic. *Thor spinosus* and *Lysmata trisetacea* range from the eastern Pacific to the Indo-West Pacific, and *Thor amboinensis* is circumtropical. Only *Hippolyte williamsi*, *Heptacarpus yaldwyni*, and *Lysmata galapagensis* are endemic and distinct.

The hippolytid fauna of temperate South America is depauperate compared with that of North America. Except for *Leontocaris pacificus*, the only representative of this genus in the eastern Pacific, all of the species belong to genera present in tropical or temperate areas of the northern hemisphere. Four species of *Lebbeus* live on the continental slopes.

Hippolytids of the eastern Pacific inhabit a wide range of depths and habitats. Species of *Spirontocaris*, *Lebbeus*, and *Eualus* prefer habitats from the lowest intertidal zone to the

Table 1
Ranges of Hippolytid species in the eastern Pacific.

Bering Sea, Aleutian Island or Alaskan Mainland to Southern California, USA, or Baja California, Mexico

Eualus avinus
E. barbatus
E. berkeleyorum
E. biunguis
E. fabricii
E. lineatus
E. macrophthalmus
E. pusiolus
E. suckleyi
E. townsendi
Hippolyte californiensis
H. clarki
Lebbeus brandti
L. catalepsis
L. grandimanus
L. groenlandicus
L. polaris
L. possjeticus
L. schrenki
L. vicinus
L. washingtonianus
L. zebra
Heptacarpus brevirostris
H. camtschaticus
H. carinatus
H. decorus
H. flexus
H. herdmani
H. kincaidi
H. littoralis
H. moseri
H. paludicola
H. pugettensis
H. sitchensis
H. stimpsoni
H. stylus
H. taylori
H. tenuissimus
H. tridens
Spirontocaris arcuata
S. holmesi
S. lamellicornis
S. ochotensis
S. prionota
S. sica
S. snyderi
S. truncata

Central California to Baja California

Heptacarpus brachydactylus
H. franciscanus
H. fusemaculatus
H. palpator
H. pictus
Lebbeus lagunae
Lysmata californica (south to Galapagos)

Gulf of California to Northern Peru

Heptacarpus yalduwyni
Hippolyte williamsi
H. zostericola
Latreutes antiborealis (south to Chile)
Lysmata galapagensis
L. intermedia
L. trisetacea
Thor algicola
T. amboinensis
T. spinosus
Trachycaris restrictus

Peru–Chile

Lebbeus bidentatus
L. carinatus
L. scrippsi
L. splendidus
Eualus dozei
Leontocaris pacificus
Lysmata porteri

continental slopes. Species of *Lebbeus* are the deepest eastern Pacific hippolytids, living as deep as 2824 m. Except for *Heptacarpus yalduwyni*, species of *Heptacarpus* usually range from the upper intertidal zone to the continental shelf. Species of *Hippolyte* live in shallow water with sea grasses or beds of algae. Species of *Lysmata* live in tidepools or in cracks and caves among coral or rocks from the intertidal zone to shallow subtidal areas. *Thor amboiensis* tends to associate with subtidal cnidarians. *Thor algicola*, *Thor spinosus*, *Trachycaris restrictus*, and *Latreutes antiborealis* live among algae or on subtidal bottoms of sand, rock, coral, or rubble. *Leontocaris pacificus* lives on the continental slope.

Classification of the hippolytid shrimp is in flux. According to Williams (1984), species of the family are characterized by having the first two pairs of legs chelate, the first pair not much stronger than the rest, the carpus of the second pair of legs subdivided, the eyes well developed and not covered by the carapace, and the mandibles usually deeply cleft. A recent cladistic analysis by Christoffersen (1988) splits the Hippolytidae into at least seven families and divides them among two superfamilies, the Crangonoidea and the Alpheoidea. However, this analysis did not provide familial placement for all of the genera considered to belong to the traditional family Hippolytidae and provided no key to the groups. Reinterpretation of some of the genera of hippolytids, such as *Eualus*, also is being considered by Christofferson and others.

Despite the confusion surrounding the systematic relationships among hippolytids, it seems useful to provide a key to the species. The last comprehensive key to the species of the northeastern Pacific was prepared by Rathbun (1904); the most recent extensive synonymy and list of species was included in the work of Holthuis (1947). More recent keys are available for British Columbia (Butler 1980), the Gulf of California (Wicksten 1983), and Peru (Mendez 1981). Illustrations and keys to intertidal species have been provided in accounts of the fauna of Puget Sound and adjacent areas (Kozloff 1974), California (Ricketts et al. 1985; Smith and Carlton 1975; Chace and Abbott 1980) and the Gulf of California (Brusca 1980; Kerstitch 1989). Fourteen new species have been described since 1947 (Butler 1971, 1980; Jensen 1983, 1987; Kobyakova 1967; Wicksten and Butler 1983; Wicksten and Mendez 1982; Wicksten 1984, 1986, 1987a; Zarenkov 1976).

The following key includes all hippolytid species reported from the Aleutian Islands (south of the Bering Sea) to Cape Horn, excluding the Straits of Magellan. The arrangement in the key is artificial. Geographic and depth ranges are provided. Superscript numbers in parentheses at the ends of couplets refer to notes following the key, where further information on ranges, synonyms, and species of uncertain classification can be found.

Key to the Hippolytidae

1 Lateral surface of carapace with many scattered spines. Carpus of second pereopods with 2 segments ..... ***Trachycaris restrictus* (A. Milne-Edwards)**
Eastern Atlantic from Canary Islands to St. Helena Island, Bermudas, to Brazil, Gulf of California, Panama; 0–100 m (Wicksten 1983).

Lateral surface of carapace with at most three spines. Carpus of second pereopods with 3 or more segments 2

2 Carpus of second pereopods with 3 segments. (Often associated with sea grasses or brown algae) 3

Carpus of second pereopods with 4 or more segments. (Size and associations various) 7

3 Rostrum deep, lamellate. Anterior margin of carapace with 10 spines. No hepatic spine ..... ***Latreutes antiborealis* Holthuis**
Gulf of California to Chile, 4–46 m (Wicksten 1983).[1]

Rostrum elongate. Anterior margin of carapace with 2 spines. One hepatic spine 4

4 First antennular segment without outer distal spines 5

First antennular segment with one or more outer distal spines 6

5 Tip of rostrum trifid. (Usually found among giant kelp, *Macrocystis* spp.) ..... ***Hippolyte clarki* Chace**
Sheep Bay, Alaska to Cedros Island, Baja California, 0–10 m (Wicksten 1983).

Tip of rostrum bifid. (Usually found among sea grasses) ..... ***Hippolyte zostericola* (Smith)**
Massachusetts to Curacao, western Colombia, shallow subtidal (Wicksten 1989).

6 First segment of antennular peduncle with one (rarely 2) spines, rostrum of female reaching nearly as far as tip of scaphocerite ..... ***Hippolyte californiensis* Holmes**
Sitka, Alaska to Baja California; rare in Gulf of California, 0–10 m, usually among eelgrass (*Zostera* sp.) (Wicksten 1983).

First segment of antennular peduncle with 3 spines, rostrum of female reaching about to distal 1/3 of scaphocerite ..... ***Hippolyte williamsi* Schmitt**
Gulf of California to Chile, 0–10 m, among rocks and brown algae (*Sargassum* sp.) (Wicksten 1983).[2]

7 Carpus of second pereopod with 4 segments. Left second pereopod longer and stronger than right ..... ***Leontocaris pacificus* Zarenkov**
Off Chile, 600–700 m (Zarenkov 1976).

Carpus of second pereopod with 6 or more segments. Left and right second pereopods equal or nearly so 8

8 Carpus of second pereopod with 6 segments. (Rostrum reaching at most to end of eye. Ranging from Gulf of California to Panama) 9

Carpus of second pereopod with 7 or more segments. (Rostrum reaching end of eye or beyond, found north of Gulf of California to Chile) 11

9 Supraorbital spine present. Finely striped, with large bluish-red eyespots on third abdominal tergite ..... ***Thor spinosus* Boone**
Indo-Pacific to Gulf of California, subtidal (Bruce 1976, Wicksten 1983).

Supraorbital spine absent. Translucent, mottled or spotted, without eyespots 10

10 Brightly colored with pattern of bold white spots on dark background. Anterolateral margin of carapace angular. (Symbiotic with sea anemones or corals) ..... ***Thor amboinensis*** **Heller**
Tropical Atlantic and Indo-Pacific, Cocos Island and Panama. Subtidal (Chace 1972; Abele and Patton 1976).[3]

Camouflaged, translucent to mottled like algae. Anterolateral margin of carapace rounded. (Not symbiotic with sea anemones or corals) ..... ***Thor algicola*** **Wicksten**
Gulf of California to Panama, 0–20 m (Wicksten 1987a).[4]

11 Carpus of second pereopod with 7 segments. Flagellum of antennae not as long as body. (Color in life various, often camouflaged) **12**

Carpus of second pereopod with more than 7 segments. Flagellum of antenna as long as body. (Color in life often red striped) **69**

12 More than 1 supraorbital spine **13**

One or no supraorbital spines **20**

13 Rostrum with 3–4 supraorbital spines **14**

Rostrum with 2 supraorbital spines **15**

14 Rostrum deep, subcircular; with 10–26 mostly small dorsal spines on rostrum proper and 3–4 dorsal carapace spines, ventral margin of third pleuron acute or bluntly pointed .....
..... ***Spirontocaris prionota*** **(Stimpson)**
Bering Sea to SW of San Carlos Point, Baja California, 4–163 m (Butler 1980).[5]

Rostrum moderately deep, with 1–3 large dorsal spines, truncate apex; pleuron of third somite rounded ..... ***Spirontocaris truncata*** **Rathbun**
Strait of Georgia to SW of San Carlos Point, Baja California, 37–92 m (Wicksten 1984).

15 Rostrum with styliform distal projection, no process on inner surface of eyestalk. (Usually found on offshore soft bottoms) **16**

Rostrum without styliform distal projection, process present on inner surface of eyestalk. (Found among rocks or soft bottoms) **17**

16 Distal projection of rostrum with 1 ventral spine; epipods on first and second pereopods. (Usually living at 150 m or less) ..... ***Spirontocaris holmesi*** **Holthuis**
Yes Bay, Alaska to San Diego, California, 24–386 m (Butler 1980).[6]

Distal projection of rostrum without ventral spine; epipods on first pereopods only. (Usually living at 150 m and deeper) ..... ***Spirontocaris sica*** **Rathbun**
Restoration Bay, British Columbia to between San Benito Islands and Cedros Island, Baja California; 88–849 m (Butler 1980, Wicksten 1987b).

17 Pleura of first to third somites ventrally acute or bluntly pointed, dactyls of third to fifth pereopods long, slender, with acute tips ..... ***Spirontocaris lamellicornis*** **(Dana)**
Bering Sea to Santa Monica Bay, California, 3–192 m (Butler 1980, Standing 1981).

Pleura of first to third somites broadly rounded ventrally, dactyls of third to fifth pereopods short and stout with bifid tips **18**

18 Body slender to moderately stout, shell thin; epipods on first and second pereopods .....
..... ***Spirontocaris snyderi*** **Rathbun**
Queen Charlotte Islands to San Cristobal Bay, Baja California, 4–141 m (Butler 1980).[7]

Body moderately stout to stout, shell thick; epipods on first to third pereopods **19**

19 Rostrum more or less ovoid; posterior dorsal spine on carapace located near middle of carapace ..... ***Spirontocaris ochotensis*** **(Brandt)**
Bering Sea to Vancouver Island, Japan, coast of Siberia; 0–247 m (Butler 1980).

Rostrum with lower limb broader than upper; posterior dorsal spine of carapace located on posterior third of carapace ..... ***Spirontocaris arcuata*** **Rathbun**
Arctic to Sea of Japan and Strait of Juan de Fuca, 5–641 m (Butler 1980).

20 (12) One supraorbital spine **21**

No supraorbital spine **36**

21 Epipods on only first pereopods **22**

Epipods on at least first and second pereopods **23**

22 Rostrum with 6–8 dorsal spines, stylocerite not reaching end of first segment of antennular peduncle ..... ***Lebbeus vicinus vicinus*** **(Rathbun)**
North of Unalaska, Aleutian Islands, 570–750 m (Rathbun 1904).

Rostrum with 3–4 dorsal spines, stylocerite reaching end of first segment of antennular peduncle ..... ***Lebbeus vicinus montereyensis*** **Wicksten and Mendez**
Monterey Bay to Gulf of California, 954–2824 m (Wicksten and Mendez 1982).

23 Epipods on first and second pereopods **24**

Epipods on at least first to third pereopods **28**

24 Carapace with 4 large dorsal spines posterior to orbit. (Often associated with sea anemones) ..... ***Lebbeus grandimanus*** **(Brazhnikov)**
Bering Sea to Sea of Japan and Puget Sound, Washington, 6–180 m (Butler 1980, Wicksten and Mendez 1982).

Carapace with 1–2 dorsal spines posterior to orbit. (Associations various or not known) **25**

25 Dactyl of third pereopod simple, without spines ..... ***Lebbeus scrippsi*** **Wicksten and Mendez**
Southern Peru to off Arica, Chile, 768–1164 m (Wicksten and Mendez 1982).

Dactyl of third pereopod with spines **26**

26 First segment of antennular peduncle with 2 anteroexternal spines. Rostrum with 5–9 ventral spines ..... ***Lebbeus splendidus*** **Wicksten and Mendez**
Off Lobos de Tierra, Peru, 712–1100 m (Wicksten and Mendez 1982).

First segment of antennular peduncle with 1 anteroexternal spine. Rostrum with 4 or less ventral spines **27**

27 Rostrum overreaching antennular peduncle, with 3–4 ventral spines ..... ***Lebbeus polaris*** **(Sabine)**
Arctic to Sea of Okhotsk, Cape Cod and northern Europe, Aleutian Islands to Alice Arm, British Columbia, 0–930 m (Green and Butler 1988).

Rostrum barely reaching end to first segment of antennular peduncle, with 1–no ventral spines ..... ***Lebbeus brandti*** **(Brazhnikov)**
Japan and Sea of Okhotsk to Wilson Bay, Alaska, 10–172 m (Wicksten and Mendez 1982).

28 (23) Epipods on first to fourth pereopods ..... ***Lebbeus carinatus*** **Zarenkov**
Off Peru and Chile, 1860 m (Zarenkov 1976).

Epipods on first to third pereopods **29**

29 Pleura of first to fifth abdominal segments ending in 1–3 spines. Four large spines on dorsal midline of carapace ..... ***Lebbeus groenlandicus* (Fabricius)**
Arctic to Cape Cod, Sea of Okhotsk, Puget Sound, 11–518 m (Butler 1980).

Pleura of at least first to third abdominal segments pointed to rounded, but not ending in 1–3 spines. One to 3 spines on dorsal midline of carapace **30**

30 Rostrum reduced to spine on frontal margin of carapace. Three spines on anterior dorsal midline of carapace **31**

Rostrum prominent, not reduced to spine. 1–2 spines on anterior dorsal midline of carapace **32**

31 Telson with 2 pair dorsal pines. No large, decurved spines below articular knobs of posterolateral margin of fourth and fifth abdominal somites ..... ***Lebbeus catalepsis* Jensen**
Strait of Juan de Fuca, low intertidal zone (Jensen 1987).

Telson with 3 pair dorsal spines. Large, decurved spines present below articular knobs of posterolateral margin of fourth and fifth abdominal somites ..... ***Lebbeus lagunae* (Schmitt)**
Pacific Grove, California to Cedros Island, Baja California, 0–74 m (Wicksten 1978, 1988).

32 Antennular peduncle extending to near middle of scaphocerite. Small subtidal species **33**

Antennular peduncle extending nearly to end of scaphocerite. Large species of continental slopes ... **35**

33 Dorsal surface of second abdominal segment without transverse furrow and fold. Rostrum not overreaching eye ..... ***Lebbeus zebra* (Leim)**
East coast of Canada, Bering Sea, Kamchatka, British Columbia, off Santa Rosa Island, California, subtidal–140 m (Wicksten and Mendez 1982).

Dorsal surface of second abdominal segment with transverse furrow and fold. Rostrum overreaching eye **34**

34 Rostrum short, not reaching end of first segment of antennular peduncle, with 2–5 dorsal spines and 1 ventral spine ..... ***Lebbeus schrencki* (Brazhnikov)**
Pribilof Islands to Sea of Japan to Passage Island, Strait of Georgia; 12–183 m (Butler 1980, Jensen and Armstrong 1987).

Rostrum reaching end of scaphocerite, with 5–7 dorsal spines and 3–4 ventral spines ..... ***Lebbeus possjeticus* Kobyakova**
Possjet Bay, USSR, Bering Island and off San Nicolas Island, California; 3–57 m (Wicksten and Mendez 1982).

35 First segment of antennular peduncle with 1 spine, bi- or trifurcated. Northern hemisphere ... ***Lebbeus washingtonianus* (Rathbun)**
Anthony Island, Queen Charlotte Islands to off San Clemente Island, California; 820–1808 m (Butler 1980).

First segment of antennular peduncle with 3 spines. Southern hemisphere ..... ***Lebbeus bidentatus* Zarenkov**
Peru and Chile, 1680 m (Zarenkov 1976).

36 (20) Third maxilliped with exopod **37**

Third maxilliped without exopod **47**

37 No epipod on any pereopod **38**

Epipod on at least on first pereopod **40**

38 Rostrum deep, shorter than carapace, eyes large ..... ***Eualus macrophthalmus*** **(Rathbun)**
Unalaska to Point Sur, California, 110–1163 m (Butler 1980).

Rostrum slender, as long as or longer than carapace, eyes smaller **39**

39 Posterior margin of third to sixth abdominal segments armed with median dorsal spine .....
..... ***Eualus barbatus*** **(Rathbun)**
Pribilof Islands to Santa Monica Bay, California, 82–507 m (Butler 1980, Wicksten 1984).

Posterior margin of third to sixth abdominal segments unarmed ..... ***Eualus biunguis*** **(Rathbun)**
Bering Sea to Sea of Japan and Oregon, 90–2090 m (Butler 1980).

40 (37) Epipods on all 3 pereopods **41**

Epipods on first and sometimes second pereopods **45**

41 Rostrum with dorsal margin markedly convex over eye, 7–14 spines ..... ***Eualus avinus*** **(Rathbun)**
Pribilof Islands to Oregon, 46–642 m (Butler 1980).

Rostrum nearly straight over eye, fewer (2–9) spines **42**

42 Rostrum not reaching second segment of antennular peduncle **43**

Rostrum reaching second segment of antennular peduncle **44**

43 Rostrum with 2–5 dorsal teeth, telson with 3–4 pair dorsolateral spines. First pereopod slender, merus about 5× as long as wide ..... ***Eualus pusiolus*** **(Krøyer)**
Bering Sea to British Columbia and Sea of Japan, Gulf of St. Lawrence to Cape Cod, northern Europe to Spain, 0–1381 m (Butler 1980).

Rostrum with 1–3 dorsal teeth, telson with 3 pair dorsolateral spines. First pereopod stout, merus about 1.6× as long as wide ..... ***Eualus dozei*** **(A. Milne-Edwards)**
Chile-Cape Horn, 13–300 m (Holthuis 1952).

44 Pleuron of fourth abdominal segment with ventral spine ..... ***Eualus lineatus*** **Wicksten and Butler**
Sitka, Alaska to Gulf of California, 18–232 m (Wicksten and Butler 1983, Wicksten 1988).[8]

Pleuron of fourth abdominal segment without spine ..... ***Eualus berkeleyorum*** **Butler**
Pribilof Islands to off Trinidad Harbor, California, 46–384 m (Butler 1980, Wicksten 1984, Jensen and Armstrong 1987).

45 (40) Normal size epipods on first and second pereopods ..... ***Eualus townsendi*** **(Rathbun)**
Pribilof Islands to Sea of Japan and Puget Sound, 38–630 m (Butler 1980).

Normal or reduced epipods on first pereopods, second pereopods with reduced epipods if present **46**

46 Most of distal part of rostrum lacking spines on dorsal margin ..... ***Eualus fabricii*** **(Krøyer)**
Bering Sea to Sea of Japan and British Columbia, northwest Atlantic Ocean south to Massachusetts Bay, 4–255 m (Butler 1980).

Distal half of rostrum with dorsal spines ..... ***Eualus suckleyi*** **(Stimpson)**
Bering Sea to Sea of Okhotsk and Grays Harbor, Washington, 11–1025 m (Butler 1980).

47 (36) Ventral margin of fourth pleuron without spine **48**

Ventral margin of fourth pleuron with spine **59**

48 Epipod absent on third maxilliped ..... ***Heptacarpus tenuissimus*** **Holmes**
Bird Island, Alaska to Santa Catalina Island, California, 2–137 m (Butler 1980).[9]

Epipod present on third maxilliped **49**

49 Epipods present on first and second or first to third pereopods **50**

Epipods absent from all pereopods **52**

50 Epipods present on first to third pereopods ..... ***Heptacarpus carinatus*** **Holmes**
Dixon Harbor, Alaska, to Point Loma, California, 0–27 m (Butler 1980).

Epipods present on first and second pereopods **51**

51 Posterior margin of third abdominal segment produced, forming rounded carina. Rostrum at least as long as carapace, with 5–8 ventral teeth ..... ***Heptacarpus flexus*** **Rathbun**
Bering Sea to Farallon Islands, California, 37–172 m (Schmitt 1921).[10]

Posterior margin of third abdominal segment not produced. Rostrum shorter, not reaching end of scaphocerite, with 1 ventral tooth ..... ***Heptacarpus herdmani*** **(Walker)**
"Puget Sound" (Wicksten and Butler 1983).

52 (49) Pterygostomian spine absent **53**

Pterygostomian spine present **55**

53 Rostrum shorter than carapace, distal ventral half convex .... ***Heptacarpus brachydactylus*** **(Rathbun)**
Monterey Bay to off Santa Cruz Island, California, 486–763 m (Standing 1981).

Rostrum longer than carapace, distal ventral half not convex or only slightly so **54**

54 Rostrum overreaching scaphocerite, without dorsal teeth on distal half .....
..... ***Heptacarpus stylus*** **(Stimpson)**
Chichagof Island, Alaska to Puget Sound, 0–439 m (Butler 1980).

Rostrum barely exceeding scaphocerite, with dorsal teeth on distal half .....
..... ***Heptacarpus franciscanus*** **(Schmitt)**
San Francisco Bay, California, to Todos Santos Bay, Baja California, 5–14 m (Schmitt 1921, Carvacho and Olson 1984).

55 (52) Rostrum with tiny lateral spinule on each side, located laterally near base.....
..... ***Heptacarpus yaldwyni*** **Wicksten**
Off Salina Cruz, Mexico, 1052–1145 m (Wicksten 1984).

Rostrum without tiny lateral spinule on each side **56**

56 Scaphocerite shorter than carapace; sixth abdominal somite longer than telson.....
..... ***Heptacarpus decorus*** **(Rathbun)**
Gabriola Island, Strait of Georgia to San Diego, California, 22–313 m (Butler 1980).

Scaphocerite as long as or longer than carapace; sixth abdominal somite shorter than telson **57**

57 Three spines on carapace and rostrum; none anterior to eye..... ***Heptacarpus tridens*** **(Rathbun)**
Aleutian Islands to Cape Flattery, Washington, 0–110 m (Butler 1980).

Five to six spines on carapace and rostrum, extending anterior to eye..... **58**

58 Dorsal posterior margin of third abdominal somite prominent; third maxilliped extending to middle of scaphocerite ..... ***Heptacarpus camtschaticus*** **(Stimpson)**
Bering Sea to Tokyo Bay and Strait of Georgia, 0–108 m (Butler 1980).

Dorsal posterior margin of third abdominal somite flattened, third maxilliped extending almost to end of scaphocerite ..... ***Heptacarpus kincaidi*** **(Rathbun)**
East coast of Vancouver Island to San Pedro, California, 10–183 m (Butler 1980).

59 (47) Epipod only on first pereopod **60**

Epipods on first and second, or first to third pereopods **62**

60 Pterygostomian spine absent ..... ***Heptacarpus littoralis*** **Butler**
Baranof Island, Alaska to Seattle, Washington, 0–18 m (Butler 1980, Jensen and Armstrong 1987).

Pterygostomian spine present **61**

61 Outer antennular flagellum extending beyond scaphocerite by about half length of former; lower limb of rostrum broader than upper ..... ***Heptacarpus moseri*** **(Rathbun)**
Bering Sea to Destruction Island, Washington; 0–1100 m (Butler 1980).

Outer antennular flagellum barely extending beyond scaphocerite; lower limb of rostrum scarcely broader than upper ..... ***Heptacarpus sitchensis*** **(Brandt)**
Resurrection Bay, Alaska, to Yaquina Bay, Oregon, 0–12 m (Butler 1980).

62 (59) Epipods on first and second pereopods **63**

Epipods on first to third pereopods **65**

63 Rostrum barely reaching end of first segment of antennular peduncle .....
..... ***Heptacarpus pugettensis*** **Jensen**
Seattle, Washington to near Morro Bay, California, intertidal (Jensen 1983, Wicksten 1988).

Rostrum exceeding end of first segment of antennular peduncle, reaching to end of entire antennular peduncle or beyond **64**

64 Rostrum usually reaching to end of scaphocerite but at least to base of antennular flagellum, ventral teeth of rostrum widely spaced ..... ***Heptacarpus paludicola*** **Holmes**
Tava Island, Alaska, to San Diego, California, 0–10 m (Butler 1980).

Rostrum reaching end of or barely exceeding antennular peduncle, ventral teeth of rostrum crowded
..... ***Heptacarpus pictus*** **(Stimpson)**
San Francisco Bay, California, to off Thurloe Head, Baja California, 0–19 m (Wicksten 1988).

65 (62) Dactyls of pereopods 3–5 simple and falcate, rostrum slightly ascending over eye and with dorsal teeth most thickly set in proximal half ..... ***Heptacarpus stimpsoni*** **Holthuis**
Sheep Bay, Alaska, to WSW of Punta Abreojos, Baja California, 0–73 m (Butler 1980, Wicksten 1988).[11]

Dactyls of pereopods 3–5 bifid and with small spines on flexor margin, rostrum not slightly ascending over eye and with dorsal teeth more widely spaced **66**

66 Rostrum not reaching as far as cornea of eye, with series of teeth angled downward from anterior margin of carapace to tip ..... ***Heptacarpus taylori*** **(Stimpson)**
Queen Charlotte Sound, British Columbia, to Magdalena Bay, Baja California, 0–13 m (Green and Butler 1988).

Rostrum exceeding cornea of eye, rostral teeth more widely spaced and not as clearly angled downward **67**

67 Spine on distal ventral flexor margin of merus of first pereopod .....
..... ***Heptacarpus fuscimaculatus*** **Wicksten**
Santa Rosa Island, California, to Guadalupe Island, Mexico, 0–295 m (Wicksten 1986, 1988).

No spine on distal ventral flexor margin of merus of first pereopod **68**

68 Rostrum usually with bifid or trifid tip, exceeding cornea, merus of third and fourth pereopods with 2 spines ..... ***Heptacarpus palpator*** **(Owen)**
Monterey Bay, California, to Isla Espiritu Santo, Gulf of California, 0–37 m (Wicksten 1986).

Rostrum usually with simple tip, not exceeding cornea, merus of third and fourth pereopods with 1 spine ..... ***Heptacarpus brevirostris*** **(Dana)**
Attu, Aleutian Islands, to Santa Cruz, California, 0–128 m (Butler 1980, Wicksten 1986).

69 (11) Dorsolateral antennular flagellum with accessory branch (may be free or partially fused with flagellum) **70**

Dorsolateral antennular flagellum without accessory branch (may be completely fused with flagellum) **72**

70 Rostrum with 12 ventral teeth. (Rostrum with 4 dorsal teeth, 23 segments in carpus of second pereopod) ..... ***Lysmata trisetacea*** **(Heller)**
Red Sea to Hawaiian Islands, Gulf of California to Malpelo Island, 0–150 m (Wicksten 1983).

Rostrum with 1–5 ventral teeth. (Rostrum with 5–8 dorsal teeth, 17–30 segments in carpus of second pereopods) **71**

71 17 Segments in carpus of second pereopods. Rostrum with 1 ventral tooth. In life, with white vertical stripes on abdomen ..... ***Lysmata galapagensis*** **Schmitt**
Magdalena Bay, Baja California, and Gulf of California to Galapagos Islands, 0–10 m (Wicksten 1983).

Carpus of second pereopod with 23–30 segments. Rostrum with 4–5 ventral teeth. In life, without white vertical stripes on abdomen ..... ***Lysmata intermedia*** **(Kingsley)**
Florida Keys to Tobago and Curacao, Azores, Gulf of California to Galapagos Islands and Peru (Wicksten 1983).

72 26–32 segments in carpus of second pereopods. Pterygostomian spine present ..... ***Lysmata californica*** **(Stimpson)**
Tomales Bay, California, to Panama, 0–10 m (Wicksten 1983).

21–22 segments in carpus of second pereopods. Pterygostomian spine absent ..... ***Lysmata porteri*** **(Rathbun)**
Chile, Juan Fernandez Islands (Holthuis 1952).[12]

Notes

[1]Rios and Carvacho (1982) reported *L. parvulus* (Stimpson) from the Gulf of California, and stated that *L. antiborealis* could be a synonym of the former species. However, they gave no justification for the synonymy. The two species are treated here as amphipanamic sibling species.

[2]*Hippolyte mexicana* Chace, 1937 is a synonym (Wicksten 1983).

[3]*Thor algicola* is a sibling species of *T. manningi* Chace, 1972. It was misidentified as *T. paschalis* (Heller) in previous works.

[4]*Thor amboinensis* has been collected at Isla Manuelita, Cocos Island, 20 m, among coral slabs and rock, 16–25 November 1989, Alex Kerstitch, 1 ovigerous female, University of Southern California collections (USC).

[5]The southernmost record of *S. prionota* is 6.5 mi. SW of San Carlos Point, Baja California (29°33′13″N, 115°36′07″W–29°33′30″N, 115°33′38″W), 37 m, rock dredge, 25 April 1950, *Velero IV* sta. 1944–50, 2 specimens, USC.

[6]*Spirontocaris bispinosa* Holmes is a synonym of *S. holmesi* Holthuis, 1947.

[7]The southernmost record of *S. snyderi* is San Cristobal Bay, Baja California (27°24′28″N, 114°39′40″W–27°26′00″N, 114°37′30″W), 75 m, 27 April 1950, *Velero IV* sta. 1949–50, 1 specimen, USC.

[8]*Eualus lineatus* has been given the name *E. herdmani* in the past due to confusion with *Heptacarpus herdmani* (Walker) (Wicksten and Butler 1983). *Eualus subtilis* Carvacho and Olson, 1984 also is a synonym (Wicksten 1988).

[9]*Spirontocaris gracilis* (Stimpson) and *Hippolyte amabilis* Lenz are synonyms of *Heptacarpus tenuissimus* (Holthuis 1947, 1969).

[10]The southernmost record of *H. flexus* is 3.2 miles from Farallon Light (37°48′N, 122°59′W), 52 m, rock, 24 Sept. 1961, *Velero III* sta. 7422, 1 specimen, USC.

[11]The southernmost record of *H. stimpsoni* is 7 mi. WSW of Point Abreojos, Baja California (26°41′ 13″N, 113°42′01″W–26°39′48″N, 113°40′43″W), 37–44 m, 29 April 1950, *Velero IV* sta. 1053–50, 1 specimen, USC. *Spirontocaris cristata* (Stimpson) is a synonym (Holthuis 1947).

[12]The revision by Chace (1972) places *Hippolysmata* in synonymy with *Lysmata*, so the species now should be called *L. porteri*.

Note: Two additional species of hippolytids have been described from Monterey Bay, California: *Hippolyte affinis* Owen, 1839 and *H. layi* (Owen 1839, in Schmitt 1921). The former species has not been found again; the latter was reported off British Columbia by Bate (1866, in Schmitt 1921). From the illustrations, the former probably should be assigned to *Spirontocaris*, the latter probably is a species of *Heptacarpus*. The type material seems to have been lost. New specimens are needed in order to resolve the relationships of these two species.

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Comparison of Fishes Taken By a Sportfishing Party Vessel Around Oil Platforms and Adjacent Natural Reefs Near Santa Barbara, California

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Since 1958, 29 oil platforms have been sited in the southern California Bight of which 28 still remain in place. However, with the exception of a few papers (Carlisle et al. 1964, Bascom et al. 1976, Allen and Moore 1976), little is known of the fish populations surrounding these structures, particularly those sited in water deeper than 30 m. Moreover, except for a brief reference in Carlisle et al., no scientific papers have been published on the use of southern California platforms by sport fishermen.

In the course of research on the Santa Barbara, California, party vessel sport fishery, it was noted that the platforms off Santa Barbara supported considerable sportfishing activity. Those platforms, located to the southeast of Santa Barbara in depths of 48–62 m (Fig. 1), were particularly important and were fished intensively for various rockfishes (genus *Sebastes*). When fishing a platform, the vessel pulled up to within 5–10 m of a platform and drifts along one side, with the vessel operator using intermittent power to keep it near the structure. Most of the desirable species, particularly rockfishes, remained close to the platforms, rarely venturing more than perhaps 20 m from the structure. The party vessels also spent considerable time fishing over nearby natural reefs. In this survey, it was noted that there appeared to be differences in species catch composition and fish size between oil platforms and these natural reefs.

Increased offshore oil drilling off California has raised interest in the role platforms play in marine systems. Questions have been raised regarding what fish live around platforms, how these structures influence populations over surrounding reefs, and whether the platforms act as fish enhancers (promoting recruitment) or only as aggregators. These questions are particularly relevant when the platforms are to be decommissioned and the possibility of allowing them to remain as artificial reefs is raised. This paper describes the results of our study on the fish populations around oil platforms and nearby natural reefs off Santa Barbara.

Methods

The study was conducted aboard the 16-m sportfishing vessel *Hornet*, berthed in Santa Barbara. During the course of this study the *Hornet* operated 6 days per week; 3 three-quarter day trips (7 am–3 pm) and 3 half-day trips (7 am–noon, 12:30 pm–5:30 pm). The *Hornet* carried a maximum of 40 passengers. Fish taken aboard the *Hornet* were sampled weekly from April 1975 to April 1978. All fish landed were measured, even those returned alive to the water as undesirable or in compliance with bag or size-limit regulations. Each was placed on a plastic measuring sheet and the length marked. Total length was recorded to the nearest mm for all fish except members of the jack (Carangidae) and mackerel (Scombridae) families, for which fork length was taken to the nearest mm. Also recorded were the number of anglers aboard the vessel, hours fished, and the location and depth of fishing effort. Of particular importance was the total time the *Hornet* fished around or over all the fishing sites. This information was obtained through biweekly interviews with *Hornet* operators throughout the 3-year survey.

Data from this study could not give an unbiased estimate of species composition. Most angling involved fishing with live bait (primarily northern anchovies *Engraulis mordax*) or with lures simulating fishes or small crustaceans at the three sites used in this study. Thus, because the sample was biased toward relatively large-mouthed, piscivorous species, we determined distributional patterns of whatever species were taken by these methods, rather than describing entire fish communities.

For this report we have divided the study sites into three locations (Fig. 1): 4 Mile Reef, 6 Mile Reef, and five platforms. Twenty-one other reefs and kelp beds located well away from this area are not included. The 4 Mile Reef is an aggregation of 1–7 m high pinnacles in 40–50 m of water. The oil platforms fished included Platforms A, B, Hillhouse, Houchin, and Hogan. These are steel structures 25–45 m on the side, situated in water depths between 54 and 62 m. The 6 Mile Reef

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Fishery Bulletin, U.S. 88:599–605.

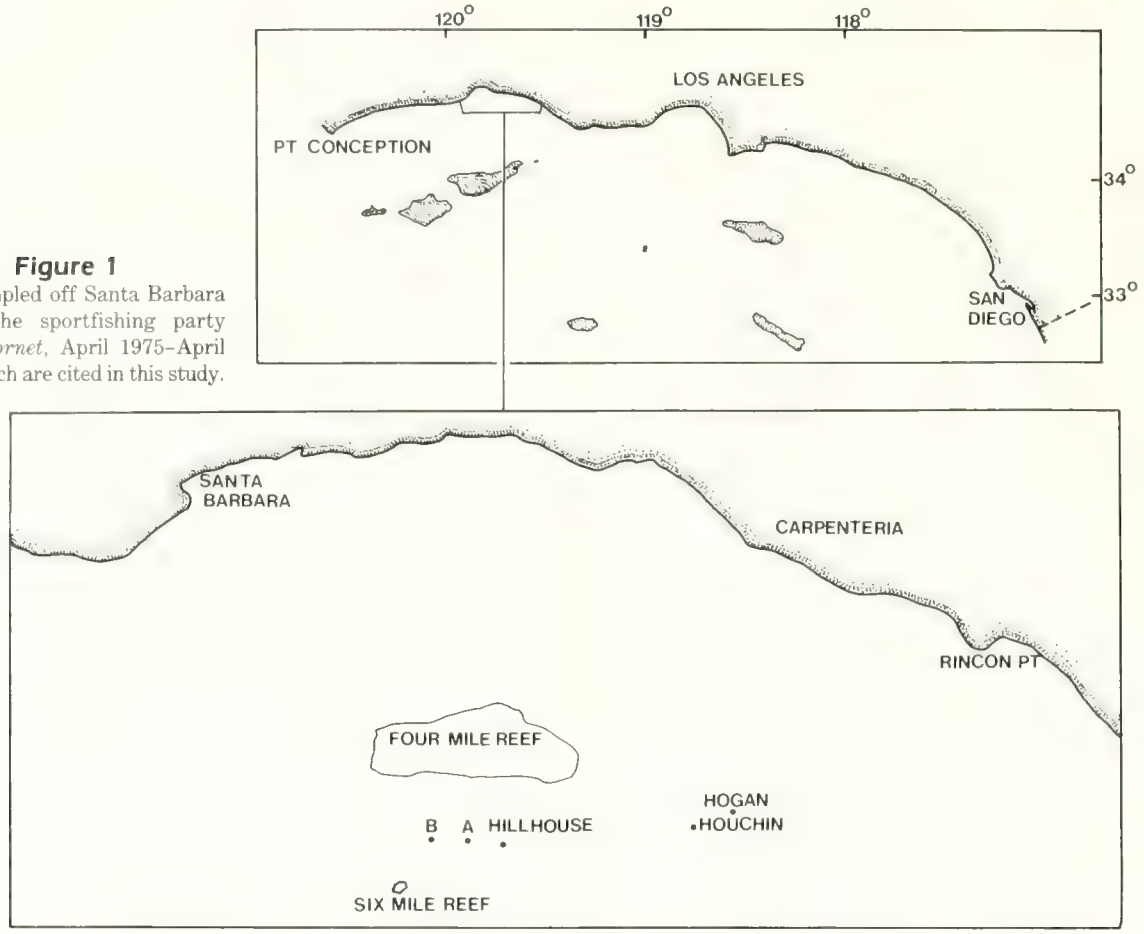


Figure 1
Sites sampled off Santa Barbara aboard the sportfishing party vessel *Hornet*, April 1975–April 1978, which are cited in this study.

is located in a depth of 74 m and rises to about 6 m above the substrata.

Results

The *Hornet* spent 18.2% of its total fishing time around the platforms, compared with 18.4% over the 4 Mile Reef and 2.4% over the 6 Mile Reef (Table 1). About 17% of all fish recorded at all 24 sites were taken around the platforms, compared with 27.6% over 4 Mile Reef and 3.2% over 6 Mile Reef (Table 2).

Twenty-eight species were taken around the platforms, compared with 34 and 17 species over the 4 Mile and 6 Mile Reefs, respectively (Table 3). Rockfishes (*Sebastes* sp.) predominated the catches at all sites in both species numbers and abundance. Of all species captured at the platforms, 53.6% were rockfishes, compared with 50% at the 4 Mile Reef and 82.4% at the 6 Mile Reef. Of all fish taken around the platform, 83% were rockfishes, compare with 96.0% and 90.8% at the 6 Mile and 4 Mile Reefs, respectively. Catch-per-unit-

Table 1
Percent of total fishing time spent off Santa Barbara at oil platforms, 4 Mile Reef, and 6 Mile Reef, April 1975–April 1978, by the sportfishing party vessel *Hornet*. Based on biweekly interviews with *Hornet* operators.

Site	Hours	% Total
4 Mile Reef	613.2	18.4
Platforms	607.6	18.2
6 Mile Reef	78.5	2.4
Other (21) sites	2039.6	61.0

Table 2
Percentage, by average, of all fish sampled off Santa Barbara aboard the sportfishing party vessel *Hornet*, April 1975–April 1978.

Site	*N*	% Total
4 Mile Reef	4 390	27.6
Platforms	2 746	17.3
6 Mile Reef	510	3.2
All Other Areas	8 272	52.0

Table 3

All fish surveyed off Santa Barbara aboard the sportfishing party vessel *Hornet*, April 1975–April 1978, around the oil platforms (A, B, Hillhouse, Houchin, and Hogan), 4 Mile Reef, and 6 Mile Reef.

Species	Total length (mm)	SD	*N*	% Total
Oil platforms[1]				
Sebastes serranoides	270.0	28.1	831	30.3
Sebastes entomelas	265.4	25.8	420	15.3
Scomber japonicus	358.3	44.8	283	10.3
Sebastes pinniger	238.8	24.3	191	7.0
Sebastes auriculatus	269.1	49.9	183	6.7
Sebastes paucispinis	260.8	32.8	147	5.4
Sebastes miniatus	262.1	37.8	143	5.2
Sebastes mystinus	243.0	27.2	128	4.7
Paralabrax clathratus	318.5	61.2	92	3.4
Sebastes hopkinsi	213.2	16.8	60	2.2
Sebastes caurinus	260.2	34.4	60	2.2
Sebastes flavidus	255.9	23.0	59	2.2
Ophiodon elongatus	490.2	136.2	17	0.6
Genyonemus lineatus	294.6	33.9	16	0.6
Trachurus symmetricus	226.5	33.1	15	0.6
Sebastes dalli	157.1	27.0	14	0.5
Medialuna californiensis	259.2	12.5	13	0.5
Paralabrax nebulifer	455.2	65.3	12	0.4
Sebastes rubrivinctus	238.7	24.7	12	0.4
Sebastes rosaceus	213.4	17.7	10	0.4
Sebastes constellatus	280.0	39.3	5	0.2
Sarda chiliensis	512.5	15.8	4	0.2
Citharichthys sordidus	208.7	11.0	3	0.1
Chromis punctipinnis	290.0	1.4	2	0.1
Scorpaena guttata	219.0	96.2	2	0.1
Scorpaenichthys marmoratus	362.5	14.8	2	0.1
Squalus acanthias	989.5	4.9	2	0.1
Sebastes umbrosus	147.0	94.8	2	0.1
Total			2728	

Species	Total length (mm)	SD	*N*	% Total
4 Mile Reef[2]				
Sebastes mystinus	259.6	35.6	1044	23.8
Sebastes hopkinsi	215.5	17.1	947	21.6
Sebastes serranoides	294.3	40.1	750	17.1
Sebastes paucispinis	298.2	58.4	716	16.3
Scomber japonicus	306.6	25.8	228	5.2
Sebastes entomelas	189.3	24.4	97	2.2
Sebastes rosaceus	197.2	23.7	97	2.2
Sebastes constellatus	287.6	44.6	60	1.4
Sebastes rubrivinctus	266.7	46.7	57	1.3
Paralabrax clathratus	334.4	85.9	54	1.2
Sebastes auriculatus	333.4	67.6	51	1.2
Sebastes miniatus	375.5	90.6	42	1.0
Ophiodon elongatus	537.3	117.9	36	0.8
Sebastes umbrosus	197.7	28.1	30	0.7
Sebastes caurinus	346.7	57.6	25	0.6
Sebastes dalli	136.9	27.9	16	0.4
Anoplopoma fimbria	216.9	2.0	14	0.3
Atractoscion nobilis	878.6	166.0	12	0.3
Chromis punctipinnis	310.6	48.4	10	0.2
Genyonemus lineatus	303.2	52.1	10	0.2
Sebastes pinniger	241.8	98.3	10	0.2
Trachurus symmetricus	272.8	20.7	9	0.2
Scorpaena guttata	253.6	43.5	7	0.2
Sebastes flavidus	255.3	33.1	7	0.2
Semicossyphus pulcher	545.8	69.0	5	0.1
Paralabrax nebulifer	531.8	61.7	5	0.1
Sebastes carnatus	218.3	13.3	4	0.1
Hydrolagus colliei	500.3	81.3	3	0.1
Medialuna californiensis	250.0	12.7	2	<0.1
Sarda chiliensis	440.5	7.8	2	<0.1
Squatina californica	1040.5	57.3	2	<0.1
Eptatretus stouti	287.0	0.0	1	<0.1
Synodus lucioceps	328.0	0.0	1	<0.1
Total			4354	

Species	Total length (mm)	SD	*N*	% Total
6 Mile Reef[3]				
Sebastes mystinus	262.5	42.3	146	28.6
Sebastes entomelas	309.7	28.0	112	22
Sebastes hopkinsi	234.0	27.0	85	16.7
Sebastes pauscispinis	307.6	60.7	75	14.7
Sebastes rubrivinctus	270.8	43.8	26	5.1
Sebastes serranoides	286.6	47.5	20	3.9
Genyonemus lineatus	301.6	21.7	17	3.3
Sebastes constellatus	267.4	70.9	5	1.0
Sebastes miniatus	387.6	57.3	5	1.0

Species	Total length (mm)	SD	*N*	% Total
Sebastes chlorostictus	205.3	22.1	4	0.8
Sebastes caurinus	357.0	58.2	3	0.6
Ophiodon elongatus	639.0	172.5	2	0.4
Sebastes flavidus	297.5	0.7	2	0.4
Paralabrax nebulifer	537.0	0.0	1	0.2
Sebastes dalli	157.0	0.0	1	0.2
Sebastes rosaceus	171.0	0.0	1	0.2
Sebastes umbrosus	186.0	0.0	1	0.2
Total			506	

[1]No. trips = 15; No. anglers = 352; No. hours fished = 47.0; Effort = 8251 angler hours; CPUE = 0.33 fish per angler hour; $H' = 1.03$.
[2]No. trips = 24; No. anglers = 454; No. hours fished = 79.8; Effort = 36 206 angler hours; CPUE = 0.12 fish per angler hour; $H' = 0.95$.
[3]No. trips = 6; No. anglers = 58; No. hours fished = 12.5; Effort = 725 angler hours; CPUE = 0.70 fish per angler hour; $H' = 0.95$.

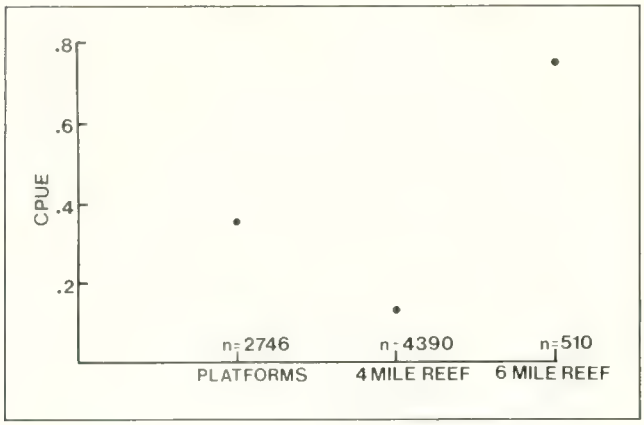


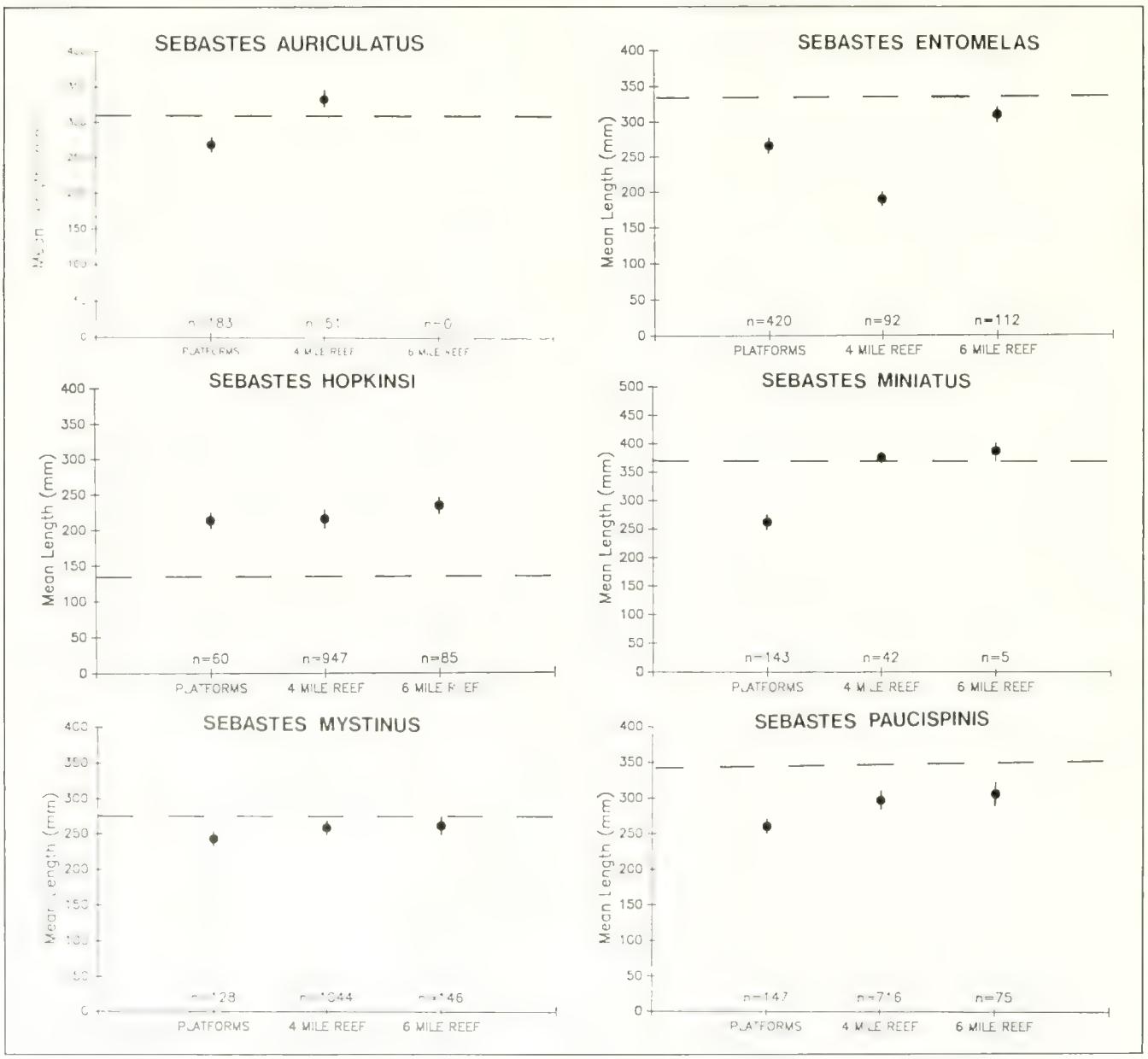
Figure 2

Catch-per-unit-effort (number of fish taken per angler hour) of all species caught aboard the sportfishing vessel *Hornet*, based on sampling during April 1975–April 1978 at three sites off Santa Barbara.

Table 4

Kendall tau rank correlation analysis of the top ten species taken by the sportfishing party vessel *Hornet*, April 1975–April 1978, at three sites off Santa Barbara, California.

6 Mile Reef	$\tau = 0.13$	
	$p = 0.26$	
	$N = 14$	
4 Mile Reef	$\tau = 0.00$	$\tau = 0.72$
	$p = 0.50$	$p = 0.01$
	$N = 14$	$N = 14$
	Platform	6 Mile Reef



effort (CPUE), defined as number of fish taken per angler hour, was highest at the 6 Mile Reef, followed by the platforms and the 4 Mile Reef (Fig. 2).

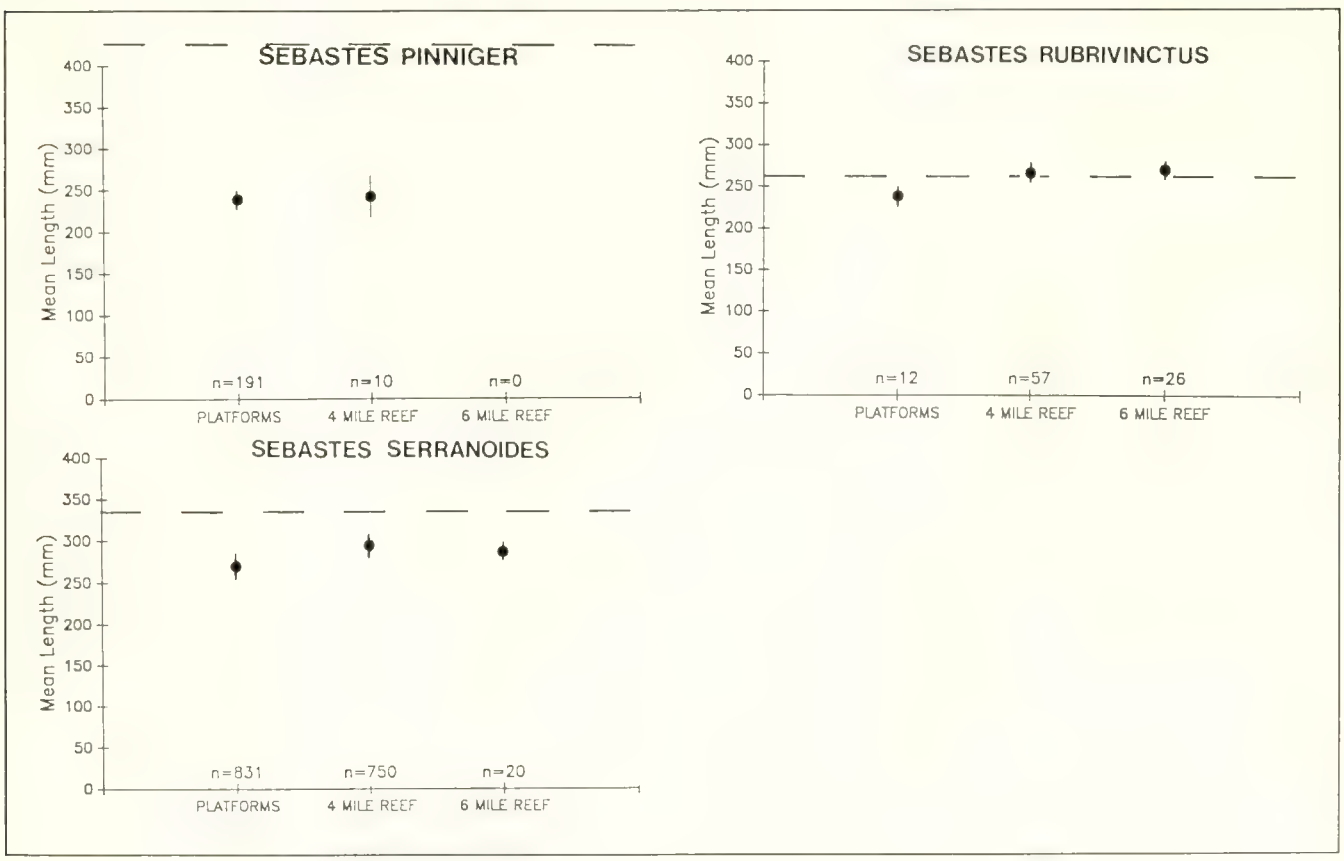
At the platforms (Table 3) rockfish made up 8 of the 10 most-frequently-taken species. While olive rockfish *Sebastes serranoides*, widow rockfish *S. entmelas*, chub mackerel *Scomber japonicus* comprised 55.9% of the total catch, a number of other species (including canary rockfish, *Sebastes pinniger*, brown rockfish *S. auriculatus*, and bocaccio *S. paucispinis* were also taken in some numbers. AT the 4 Mule Reef, 8 of the top 10 species were rockfish, with blue rockfish *Sebastes mystinus*, squarespot rockfish *S. hopkinsi*, *S. serranoides*, and *S. paucispinis* dominating the catch, making up 78.8%. Nine of the top 10 species at the 6 Mile Reef were rockfish and *S. mystinus*, *S. entomelas*, *S. hopkinsi*, and *S. paucispinis* were taken in the largest numbers, forming 82.0% of the total.

We compared the rank abundances of the top 10 species at the three sites with the Kendal tau coefficient test (Sokal and Rohlf 1969). Based on this measure, species composition was significantly correlated between natural reefs only, and species arrays from natural reefs were not correlated with that of the platform (Table 4). The primary differences between the reefs and platforms were the relative abundances of *S. hopkinsi*, *S. mystinus*, starry rockfish *S. constellatus*, and flag rockfish *S. rubrivinctus* at the natural reefs and the scarcity of *S. auriculatus* and *S. pinniger* over these reefs.

With only a few exceptions, all rockfish taken around the platforms were juveniles (Fig. 3). A major exception was *S. hopkinsi*, a species in which all individuals takn were mature. In addition, a few adult *S. auriculatus* and *S. mystinus* were caught, as well as one vermillion rockfish *S. miniatus*. At the 4 Mile Reef, a higher percentage of fish were mature. Again, all *S. hopkinsi* taken were adults, as were most *S. auriculatus* and *S. miniatus*, many *S. mystinus* and *S. rubrivinctus*, and a few *S. serranoides*. In general, more adult rockfish were taken over the 6 Mile Reef than at the other two stations. All *S. hopkinsi* were mature,

Figure 3 (bottom facing page and below)

Mean size (with 95% confidence interval) of 9 species caught aboard the sportfishing party vessel *Hornet*, based on sampling during April 1975–April 1978 at three sites off Santa Barbara. Also included are 50% lengths at maturity from data in Wyllie Echeverria (1987), Love et al. (1990), and Love (unpubl. data).



as were most *S. miniatus* and *S. rubrivinctus* and many *S. entomelas*, *S. mystinus*, *S. paucispinis*, and *S. serranoides*.

Discussion

During the period sampled, the platforms were important sites for the *Hornet*'s fishing effort. They were also fished by other sportfishing party vessels from Ventura Harbor, about 30 km to the east, though we are unsure of the total effort from these vessels. In both circumstances, these structures provided the vessel operators with a relatively reliable source of easily caught, though generally small, fish. The ease with which small rockfish were caught made the platforms particularly attractive to the *Hornet*'s operators on half-day runs, when the vessels carried many inexperienced fishermen. The platforms were also utilized when fishing was poor at other locations for more desirable species, such as kelp bass *Paralabrax clathratus*.

We have recently (1989) discussed platform fishing with current Santa Barbara party vessel operators. They report that though the platforms are still fished for small rockfish, kelp bass are an equal or more important species during summer months. This is particularly true of the eastern platforms, particularly Houchin, Hogan, and Hope (2 km east of Hogan). Though there are five platforms in this complex, only these three are routinely fished. During the season's peak, as many as 300–400 *P. clathratus* per trip are caught from around a single platform. Based on tagging studies by P. Hart (Dep. Biol. Sci., Univ. Calif., Santa Barbara 93106, pers. commun., Sept. 1988), it is likely that kelp bass move onto the platforms before summer and leave in the fall, traveling both east and west, with reported movements of as much as 32 km in 6 months.

In the study conducted between 1975 and 1978, there were significant differences in both species compositions and mean sizes between the three sites (though the natural reefs were much more similar with each other). Much of the differences in species composition between the platforms and the natural reefs came from the relative abundance of high-relief substrate-associated rockfish (such as *S. constellatus* and *S. rubrivinctus*) over the reefs and their near absence around the platforms. The substrata around these structures are composed of a mixture of drill cuttings and mussels which have broken off the platform pilings. This does not appear to be suitable habitat for many rockfish species.

On the other hand, a few substrate-associated species, such as juvenile *S. auriculatus* and *S. pinniger*, were most abundant around the platforms. *Sebastes auriculatus* (both juveniles and adults) are most often found associated with low relief or the sand-rock interface, habitat most similar to that around the platforms. We do not know what substrata juvenile *S. pinniger* prefer, though its abundance around the platforms and scarcity over natural reefs imply it favors habitats similar to *S. auriculatus*.

It is unclear why *S. mystinus* and particularly *S. hopkinsi* should be relatively uncommon around the platforms, yet abundant on the reefs. Both species are midwater planktivores, always found in association with high relief. A possibility is that both species take refuge in crevices at night and that these are relatively uncommon on the platform pilings and cross members.

Differences in depths between the sites were probably responsible for only a few of the observed differences in species abundances and sizes. The absence of *P. clathratus* from the 6 Mile Reef was undoubtedly due to the reef's relatively extreme depth. The 6 Mile Reef is situated in 74 m, well below the 46 m maximum depth of *P. clathratus* (Eschmeyer et al. 1983). Love et al (in review) summarizing ontogenetic *Sebastes* movements, noted that almost all species recruit to waters shallower than adult depth, subsequently moving to deeper water as they mature. If depth were a major factor in our study, we would expect to see the smallest rockfish at the shallowest (4 Mile Reef) station. However, while both large and small individuals of many rockfish species were taken at 4 Mile Reef, the mean size of most species (except for *S. entomelas*) was actually larger than at the other two sites.

Are the platforms we sampled aiding rockfish production or do they only act as aggregators? In other words, do rockfish recruit from the plankton to the platforms or do they settle out elsewhere and later migrate to these structures? Though our data is not sufficient to answer the question, there is evidence that at least some recruitment takes place around Santa Barbara platforms. In the only detailed study of a California platform, Carlisle et al. (1964) found that both *S. paucispinis* and *S. serranoides* recruited to platform Hazel, located in 30 m of water, about 6 km inshore of our study platforms. We believe it is likely that some rockfish species (i.e., *S. entomelas*, *S. mystinus*, *S. paucispinis*, *S. pinniger*, and *S. serranoides*) recruit to our platforms, particularly in light of the large numbers of small fish, most only 1–2 years old. Smaller and younger fish may be present at these platforms, but their small size precludes their being taken by hook-and-line.

There are several reasons that mature rockfish are rare around the platforms. While juveniles of deep-water species (i.e., *S. entomelas*, *S. pinniger*, *S. paucispinis*) are able to tolerate the warm shallow waters around these structures, the adults are not (Love et al.,

In review). Their subadults make ontogenetic shifts into deeper water. Secondly, fishing pressure around the platforms probably crops many larger individuals. Lastly, it is possible that artificial habitat in some unknown way discourages adult rockfish. F. Matthews (Dep. Oceans and Fish., Pacific Biol. Stn., Nanaimo, B.C., Canada V9R 5K6, pers. commun., May 1989) found that only immature rockfish occurred on an artificial reef in Puget Sound. Natural reefs supported both juveniles and adults.

As discussed before, most rockfish species (including *S. entomelas* and *S. paucispinis*) recruit to shallow water, then migrate into deeper zones as they mature. Based on catch rates, we have noted on several occasions that large aggregations of these species were present around the platforms for months, only to suddenly disappear. Hartmann (1987) tagged juvenile *S. paucispinis* around these platforms and noted recoveries from as much as 148 km away. In all cases the fish were taken in water considerably deeper than tagging depths. Thus, it is quite possible that some rockfish species settle out around these platforms, live there for a few years, and leave for deeper adult habitats, perhaps at considerable distances from the original recruitment site.

Conclusions

Platforms were important fishing locations for the sportfishing party vessel surveyed. About 18% of its total fishing time and 17% of the total catch occurred around the platforms. This compares with about 21% of fishing time and 31% of total catch at the nearby natural reefs. Rockfish dominated the catch at both the platforms and at the natural reefs. Confirming what we had first observed, there were significant differences in catches between the platforms and natural reefs. Juvenile rockfish composed most of the platform catch, while mature rockfish were more abundant over reefs. While midwater rockfish species were abundant at both platform and natural reefs, species compositions were different, with those benthic rockfish characteristics of high-relief substrata absent or rare around the platforms.

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Problems Identifying Tuna Larvae Species (Pisces: Scombridae: *Thunnus*) from the Gulf of Mexico

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The identification of tuna larvae of the genus *Thunnus* is very difficult. Five species of the genus *Thunnus* may spawn in the Gulf of Mexico: *albacares*, *obesus*, *alalunga*, *thynnus*, and *atlanticus*. Criteria for their identification have been established by Matsumoto et al. (1972), Potthoff (1974), and by Richards and Potthoff (1974). A combination of pigment patterns and osteological characters is the criteria used. Pigment patterns are used for larvae in the 3mm-NL to 10mm-SL size range, and osteological characters are used in larvae larger than 5 mm NL just during and after notochord flexion. Larvae larger than 7 mm SL are rare and pigment characters are not as useful since juvenile pigmentation begins to obscure the larval pigmentation, and larvae less than 5 mm NL usually do not have sufficient cartilage or bone development to determine vertebral counts or first closed hemal arch location. The combination of both character sets does allow for reliable identification in most cases. Clearing and staining larvae and the subsequent osteological examination are very time-consuming, whereas pigment pattern analysis is quite fast during normal larval ichthyoplankton identification. We conduct extensive ichthyoplankton surveys of the Gulf of Mexico annually (Richards et al. 1984, Kelley et al. 1986), and it is impractical to clear, stain, and perform osteological examination on all *Thunnus* obtained. In this study we cleared, stained, and osteologically examined all *Thunnus* larvae collected in 1982 (Richards et al. 1984) to determine a baseline value for species occurrence.

Methods

A total of 362 *Thunnus* (4.5 mm NL–9.1 mm SL) larvae were examined for the presence of black pigment on the upper and lower jaw tips, along the ventral midline of the tail, along the dorsal midline, along the lateral midline, and on the caudal fin. Since these specimens had been fixed in formalin and preserved in ethanol, red pigments were no longer present. All *Thunnus* larvae taken during 1982 and a few from 1983 were utilized, except for those which were typical *T. thynnus* (possessing pigment on both the dorsal and ventral margins of the tail) or those specimens less than 4.4 mm NL. Following pigmentation examination, specimens were cleared and stained following Potthoff (1984), and vertebral counts and position of the first closed hemal arch determined. Species identification followed the criteria established by Matsumoto et al. (1972), Potthoff (1974), and by Richards and Potthoff (1974) for North Atlantic *Thunnus* species (Table 1).

Results

Of the 362 larvae, 95 larvae will not be considered further because 4 were typical *thynnus*, 11 had no tail pigment and were too small for osteological data, 61 had ventral tail pigment and were too small for osteological data, 3 were not *Thunnus*, and 16 were lost or badly damaged during the clearing and staining process. Of the remaining 267 larvae, 241 could be reliably identified (Table 2). Most of the larvae consisted of the *atlanticus* morph with ventral tail pigment (72.7%), although a few (6.0%) lacked this. Those with ventral tail pigment are inseparable from *obesus* except by osteological criteria, and those without it are inseparable from *albacares*. Only 4.9% were *obesus*, only 6.0% were *albacares*, and 2 larvae (0.7%) were *alalunga*. The remaining 26 larvae (9.7%) cannot be positively identified (Table 3). These data demonstrate the variability which can be found in these species.

Discussion

When Richards and Potthoff (1974) made a similar study, their specimens were mainly from the Caribbean Sea and Straits of Florida. They also found that the abundant species was *atlanticus*, with few *albacares* and *obesus* larvae confirmed in the western Atlantic. These results confirm this same

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Table 1
Criteria for identification of larval *Thunnus*.

	alalunga	*albacares*	*atlanticus*	*obesus*	*thynnus*
Dorsal tail pigment	No	No	No	No	Yes
Ventral tail pigment	No	No	Yes/No	Yes	Yes
Lower jaw pigment	No	Yes	Yes	Yes	Yes
Vertebrae	18+21	18+21	19+20	18+21	18+21
First hemal arch	10	11	11	11	10

Table 2
Characters of confirmed identifications of larval *Thunnus* (4.5 mm NL-9.1 mm SL). The characters of the remaining 26 unidentifiable larval *Thunnus* are given in Table 3.

No.	%	Ventral tail	Dorsal tail	Vertebrae	Haemal arch	Identification
194	72.7	Present	Absent	19+20	11	*atlanticus*
16	6.0	Absent	Absent	19+20	11	*atlanticus*
16	6.0	Absent	Absent	18+21	11	*albacares*
13	4.9	Present	Absent	18+21	11	*obesus*
2	0.7	Absent	Absent	18+21	10	*alalunga*
26	9.7	See Table 3				*Thunnus* sp.

Table 3
Characters of unidentifiable larval *Thunnus*.

No.	Ventral tail	Dorsal tail	Vertebrae	Haemal arch	Possible identity
5	Present	Absent	20+19	11	*atlanticus*
4	Present	Absent	18+21	10	*atlanticus/obesus/thynnus*
3	Absent	Absent	18+21	12	*albacares*
2	Present	Absent	19+21	11	*atlanticus/obesus*
1	Absent	Present	19+20	11	*atlanticus/thynnus*
1	Absent	Absent	19+20	10	*alalunga/albacares/atlanticus*
1	Absent	Absent	19+20	13	*alalunga/albacares/atlanticus*
1	Present	Absent	18+21	10	*obesus/thynnus*
1	Absent	Absent	20+19	11	*albacares/atlanticus*
1	Present	Absent	18+21	12	*atlanticus/obesus*
2	Present	Present	19+20	10	*atlanticus/thynnus*
2	Present	Present	19+20	12	*atlanticus/thynnus*
2	Present	Present	19+20	–	*atlanticus/thynnus*

trend for the Gulf of Mexico. Of the larvae shown in Table 2, 78.7% are definitely *atlanticus* with 10.9% *albacares* or *obesus*. The two *alalunga* were a surprise, as the adults of that species have not been taken in the Gulf of Mexico (Collette and Nauen 1983:81); but given the variability found in these larval characters, these data should not be used as unequivocal criteria for recording this species in the Gulf. We have speculated on the identity of the specimens listed in Table 3; as one can see, this speculation raises possibilities but not certainties.

Thunnus atlanticus is very common in the Gulf of Mexico and spawning is widespread as evidenced by larval data (Richards et al. 1984). *Thunnus albacares* supports a developing fishery, but spawning may not be as widespread based on our 1982 data. In future studies focusing on albacares, researchers will have to use cleared and stained specimens to confirm larval abundance reliably, since about 50% of those larvae lacking ventral tail pigment may be *atlanticus* morphs or possibly even *alalunga* (Table 2). Recently, Graves et al. (1989) have shown that small juveniles 10–21 mm

TL of *T. albacares* could be distinguished electrophoretically from *T. obesus*. In the 10–12 mm TL range, some of their specimens had ventral tail pigment and some did not, but had the *albacares* electrophoretic character. The ventral or dorsal tail pigment seen in specimens this large is the juvenile pattern and not the larval pigment pattern. Distinguishing between larval and juvenile pigmentation is very difficult in these transforming sizes, and care must be taken to document the size and nature of the pigment.

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Improved Methods for Isolation of Fish mtDNA by Ultracentrifugation and Visualization of Restriction Fragments Using Fluorochrome Dye: Results From Gulf of Mexico Clupeids

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The isolation of mitochondrial DNA (mtDNA) for studies of restriction-site polymorphisms among fish populations is achieved by either of two general methods. The methods are those of Lansman et al. (1981) which uses ultracentrifugation in cesium-chloride/ethidium-bromide gradients to separate mtDNA from nuclear DNA, and Chapman and Powers (1984) which uses low-speed centrifugations and organic extractions to precipitate mtDNA. Although the method of Chapman and Powers (1984) results in mtDNA of lesser purity, it apparently requires fewer hours to isolate mtDNA from a greater number of specimens than the method of Lansman et al. (1981), and avoids the high cost of purchasing and servicing a typical ultracentrifuge.

The technique chosen for visualization of restriction fragments depends upon the amount of mtDNA obtainable from the specimens of interest and its purity. Neither of the commonly reported techniques, such as end-labeling and ethidium-bromide staining, is specific for mtDNA. Since end-labeling is about 1000× more sensitive, a more highly purified preparation is required than for ethidium bromide. Radio-labeled hybridization probes are highly specific for mtDNA as well as very sensitive, but require many steps for preparation (Maniatis et al. 1982) and must be periodically remade. Biotinylation may provide longer-lived hybridization probes (Graves et al. 1990) but making them also requires several steps.

Here we introduce a new combination of isolation and visualization methods for mtDNA studies which incorporate attributes of some of the above techniques and which may aid investigators developing plans to begin mtDNA studies. Our approach was developed for potential use in a population study of Spanish sardine *Sardinella aurita*, as well as of other clupeids of the western Atlantic, while mindful of the need to process statistical sample sets. Incorporated in this presentation of methodology is a brief account of our initial findings on Gulf clupeids.

Materials and methods

Sample collection and preparation

Sardinella aurita and *Opisthonema oglinum* were collected aboard commercial purse seine vessels in the nearshore regions of central-west and north Florida between April and August 1989. Male and female gonads from these samples were excised fresh or semifresh and immediately stored in 10 mL of cold MSB-Ca^{++} (Table 1) for up to 7 days at 4°C. The tissue was blotted dry, weighed, minced, and then homogenized in 2 to 3 volumes of cold MSB-Ca^{++} by 5 strokes of a chilled 15-mL Dounce homogenizer. The homogenates were transferred to chilled 50-mL polyethylene centrifuge tubes after addition of disodium EDTA (0.2 M, pH 7.5) to a final concentration of 10 mM.

The homogenate was centrifuged at 800 × g for 10 minutes at 4°C after which the supernatant was decanted and respun. These two spins remove nuclei and cellular debris. Mitochondria were then pelleted by centrifugation at 20,000 × g for 20 minutes at 4°C. The pellet was washed with 10–20 mL of cold MSB-EDTA (Table 1) and repelleted by centrifugation for 15 minutes at 20,000 × g.

The pellets were suspended in 2 mL of cold STE (Table 1) and the mitochondrial membranes dissolved by adding 0.10 mL of 25% SDS, vortexing briefly and incubating at 37°C for 5–8 minutes. The entire lysate was then transferred to 3.0-mL Beckman polyallomer or polycarbonate centrifuge tubes containing enough cesium chloride (Sigma #C-3032) to produce a concentration of 1.1 g CsCl per mL of lysate as in Lansman et al. (1981). To this was added 0.133 mL of 0.025 M ethidium bromide. The solution was then mixed by inverting several times, and the refractive index of each tube adjusted to 1.389 at 20°C with CsCl or STE. Solution density at this R_f causes the DNA to float lower in the tube than at the R_f given by Lansman et al. (1981).

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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Table 1
Solutions used in isolation and purification of mtDNA.

MSB-Ca^{++}	0.21	M	Mannitol
	0.07	M	Sucrose
	0.05	M	Tris-HCl, pH 7.5
	3.0	mM	$CaCl_2$
MSB-EDTA	0.21	M	Mannitol
	0.07	M	Sucrose
	0.05	M	Tris-HCl, pH 7.5
	0.01	M	EDTA, pH 7.5
TE	10	mM	Tris-HCl, pH 8.0
STE	10	mM	Tris-HCl, pH 8.0
	100	mM	NaCl
	1	mM	EDTA, pH 8.0
20 × SSC	3.70	M	NaCl
	0.37	M	Na citrate, adjust pH to 7.0 with 10 N NaOH, sterilize by autoclaving
10 × TAE	0.40	M	Tris-Base
	1.15%	v/v	glacial acetic acid
	0.025	M	EDTA, pH 8.0

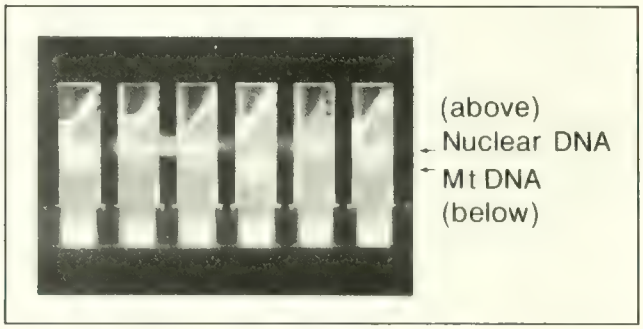

Figure 1
Appearance of nuclear and mitochondrial DNA bands in UV light after 17 hours of ultracentrifugation in CsCl/ethidium-bromide gradients at 200,000 × g and 4°C: upper bands are nuclear DNA, lower bands mtDNA. Material at the top of the tubes is the "skin" which forms during ultracentrifugation. Starting tissue was 1–2.5 g of ripe ovary from Spanish sardine *Sardinella aurita*.

Density-gradient ultracentrifugation

The cornerstone of our isolation method is low-volume ultracentrifugation using the Beckman TL-100 Tabletop Ultracentrifuge. The short rotor radius and high available g-forces of this product serve to significantly reduce spin times over current practices. The main requirement is simply to "downsize" existing protocols to be compatible with 3-mL centrifuge tubes. Isolation of mtDNA using the TL-100 appears to be less labor-intensive as well as faster in producing highly purified mtDNA than existing techniques.

Ultracentrifugation was accomplished at approximately 200,000 × g (70,000 rpm) overnight (15–17 hours) at 4°C in a fixed-angle rotor (Beckman TLA-100.3) with six positions. Deceleration was set at 5. Following ultracentrifugation the mtDNA bands, which are visible in fluorescent light 0.5–0.7 mm below the nuclear DNA bands (Fig. 1), were withdrawn using an 18-gauge stainless-steel hypodermic needle inserted through the top of the tube to a position slightly below the mtDNA band. Withdrawn sample volume was then adjusted to 0.5 mL with STE and extracted several times with NaCl-saturated n-butanol at room temperature to remove the ethidium bromide (Lansman et al. 1981).

Following butanol extraction, the mtDNA was ethanol-precipitated using essentially the procedure of Maniatis et al. (1982). Sample molar concentrations were adjusted by dilution with 0.33 mL of cold, sterile, distilled H_2O. Exactly two volumes of cold ethanol were added to the solution which is briefly vortexed. The sample is stored overnight at −20°C after which mtDNA is pelleted by centrifugation in the fixed-angle rotor in the Beckman TL-100 at 30,000 × g for 30 minutes at 2°C. After complete drying by evaporation (no odor of ethanol remaining) the mtDNA pellet is dissolved in 50 μL of cold TE (Table 1) and stored indefinitely at −20°C.

Fluorometric quantification of mtDNA

Yield quantification followed Paul and Myers (1982). Standard curves were generated from fluorescence of known DNA quantities in a 1.5×10^{-4} M solution of Hoechst 33258 (CalBiochem Cat. #SR5A03-0388). Fluorescence was measured using an Aminco J4-7439 Fluoro-Colorimeter (GE F4T4/BL UV lamp and an R-136 phototube) at photomultiplier settings of 1, 3, and 10. mtDNA concentrations were calculated using the geometric mean regression of the standard curve. Yields were determined as μg mtDNA per g of starting tissue.

Restriction endonuclease digestion

Immediately prior to digestion with restriction enzymes, samples were treated with RNAse-A to a concentration of 10 μg/mL and incubated at room temperature for 1 hour. Samples were then heated to 70°C for 5 minutes and cooled on ice before addition of the restriction enzymes. In this initial study only two six-base-pair restriction endonucleases were used: *Eco*-RI and *Hin*d-III. Digestions were carried out according to the reaction conditions specified by the manufacturers. Reaction mixtures contained 0.2–1.0 μg of mtDNA in a final volume of 20 μL adjusted with

sterile, distilled water. Using a Hamilton syringe, 2.0 μL of the digestion buffer was added to the tube and mixed by vortexing, then at least two units of the restriction enzyme were added and also mixed by vortexing. The reaction mixtures were allowed to incubate at 37°C for at least 2–3 hours, but sometimes as long as overnight. The reaction was stopped by the addition of 0.4 μL of 0.5 M EDTA (pH 7.5).

mtDNA fragment visualization using Hoechst 33258

Restriction fragments were separated on horizontal (submerged) agarose slab gels with the Hoechst 33258 fluorochrome incorporated as described in DeFlaun and Paul (1986). The fluorochrome is a 1:30 dilution of 1.5×10^{-4} M solution of Hoechst 33258 with 1 × SSC (i.e., 1:20 dilution of 20 × SSC, Table 1). The gel is created by boiling a 1.1% solution of agarose in distilled H_2O containing 10% 10 × TAE (Table 1) buffer until clear. The suspension is allowed to cool to the touch before adding a 1.1% volume of the Hoechst 33258 dilution. After casting, the gel is allowed to set for at least 30 minutes in an opaque box to prevent photo-deactivation of the fluorochrome.

For running, the gel is immersed in a tank buffer of 500 mL distilled H_2O, 56 mL of 10 × TAE (Table 1), and 5.6 mL of the Hoechst 33258 dilution. Samples containing 10 μL of digested mtDNA from the reaction mixture, 1 μL of 10 × TAE, and 2 μL of tracking dye (Bromophenol blue) are then micropipetted into the wells. Outside lanes contained *Hin*d-III digested λ-DNA standards.

Gels are electrophoresed at 50 volts for approximately 3 hours, or until the tracking dye covers three-quarters of the length of the gel. The gel apparatus remains isolated from light during running. Following the run, gels were placed on a UV transilluminator and photographed with a Polaroid MP-4 Land-camera using Polaroid Type 667 black-and-white film.

Measurement and analysis of mtDNA fragment patterns

Photographs of the gels were processed on a computer-automated optical pattern-recognition system developed by Biosonics Inc., Seattle, Washington. Fragment sizes were calculated by the global form of the reciprocal method as described by Elder and Southern (1987).

Results

Ovarian tissue from *Sardinella aurita* and *Opisthonema oglinum* consistently produced visible mtDNA bands in the CsCl/ethidium-bromide gradient by ultracentrifugation in fewer than 17 hours (Fig. 1), but the testicular tissue did not. If carefully extracted, the mtDNA fraction was sufficiently void of contamination by RNA and nuclear DNA. With the Beckman TL-100 it is undoubtedly possible to reduce the time required for ultracentrifugation even further, since higher speeds of up to 100,000 rpm are available using polycarbonate tubes.

The only apparent drawback of the fixed-angle rotor over the swinging-bucket rotor is that in the fixed-angle rotor the cross-sectional area of the fluid in the tube is greatest while under centrifugation, but becomes less when the rotor is at rest and least when the tube is upright. Thus, the scab-like material that forms on top of the gradient during centrifugation protrudes down into the gradient when the tube is upright (Fig. 1). However, if the refractive index is adjusted carefully, both DNA bands will form below the protrusion of this scab-like material. Since this material does not crumble after centrifugation at 4°C, it can be removed or pushed aside to withdraw the mtDNA.

The mean yield of mtDNA from fresh *S. aurita* gonads stored in MSB-Ca^{++} for 2 days at 4°C was 1.90 ± 0.60 μg mtDNA per g of tissue. The mean yield from fresh *S. aurita* gonads stored in MSB-Ca^{++} for 7 days at 4°C was 1.18 ± 0.45 μg mtDNA per g of tissue. The semifresh *O. oglinum* processed after 5 days of storage yielded 1.01 ± 0.66 μg mtDNA per g of ovarian tissue. Isolation of mtDNA from material quick-frozen on liquid nitrogen was also achieved, but yields were reduced by as much as 56% from that of the semifresh samples.

Various concentrations of mtDNA were electrophoresed on Hoechst 33258/agarose gels. The minimum concentration required to produce clear, resolvable restriction fragments (at the 500-base pair (bp) level) was 11.8 ng/μL in 20-μL wells. Fragment mobilities from separate digestions with the two restriction endonucleases indicated the mtDNA genome size for *S. aurita* to be 16,263–16,353 bp, and that of *O. oglinum* to be 15,186–15,683 bp.

Discussion

The techniques presented here have successfully addressed some of the potential problems associated with performing a large population study using mtDNA. Purification of sufficient quantities of mtDNA to perform a detailed restriction-site analysis has been

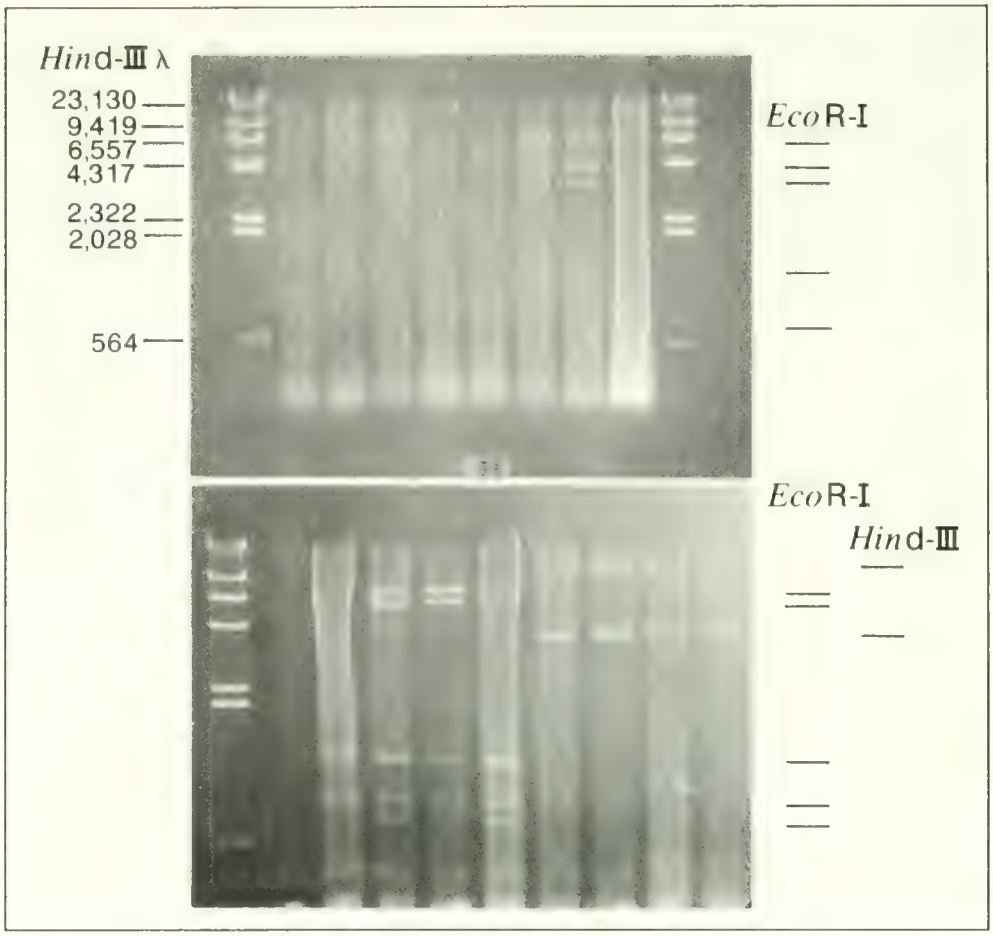

Figure 2
Top: Restriction digests with *Eco*-RI of mtDNA from Spanish sardine *Sardinella aurita* visualized on a routine Hoechst/agarose gel photographed in transilluminated UV light. Lane 1 is the *Hin*d-III digested λ-DNA standard. Bottom: *Eco*-RI (left) and *Hin*d-III digests of mtDNA of threadherring *Opisthonema oglinum*. All digests were carried out on ~0.3 μg of mtDNA for 2.5 hours, then electrophoresed for 3 hours at 50 volts. The *Hin*d-III digest of *S. aurita* mtDNA (not shown) produces five fragments compared with two for that of *O. oglinum*.

accomplished through low-volume density-gradient separation in a relatively inexpensive tabletop ultracentrifuge which is essentially portable. This simple overnight ultracentrifugation followed by extraction of the mtDNA and subsequent ethanol precipitation would allow mtDNA isolation from at least 30 individuals in a normal work-week by a single worker. Five grams of fresh, ripe, ovarian tissue should produce enough mtDNA per individual to be digested separately by 20 restriction endonucleases and still be resolved on Hoechst 33258/agarose gels.

Agarose gels incorporating the Hoechst 33258 fluorochrome (DeFlaun and Paul 1986) is a good substitute for staining of restriction fragments using ethidium bromide. Whereas Hoechst 33258 binds specifically and quantitatively to AT-rich mtDNA (Latt and Stetten 1976) ethidium bromide has mixed RNA-DNA specificity (Le Pecq and Paoletti 1966) reducing its resolving power and making visualization of small fragments (<500 bp) difficult. The suggestion of Lansman et al. (1981), that minimally 0.5 μg of mtDNA be used per digestion to insure visualization of fragments with ethidium-bromide staining, limits its resolving power to about 20 ng of DNA. In contrast, a zone of fragments containing only 7.0 ng of DNA (~1.8 μg per digestion) should be visible on Hoechst 33258/agarose gels, and these can be viewed immediately following electrophoresis on a UV transilluminator.

Our estimate of the sizes of the mtDNA genomes of *Sardinella aurita* and *Opisthonema oglinum* is close to those obtained for other clupeids (Kornfield and Bogdanowicz 1987, Avise et al. 1989). Ours are probably very good estimates since the pattern-recognition system used here greatly reduces measurement error of fragment mobility inherent in the use of stereomicroscopes and other manual methods. This survey of only a few individuals did not reveal any polymorphisms at *Eco*-RI or *Hin*d-III in either species, but the restriction fragments produced at both restriction sites are quite distinct between the species (Fig. 2). With new microextraction methods for mtDNA available (Graves et al. 1990), it should be possible to eventually separate or identify even the eggs and very young larvae of *S. aurita* and *O. oglinum* obtained in field samples. The ability to do so could be used to provide estimates of egg and larval mortality rates in the

earliest life-history stages of these and other important pelagic species.

Acknowledgments

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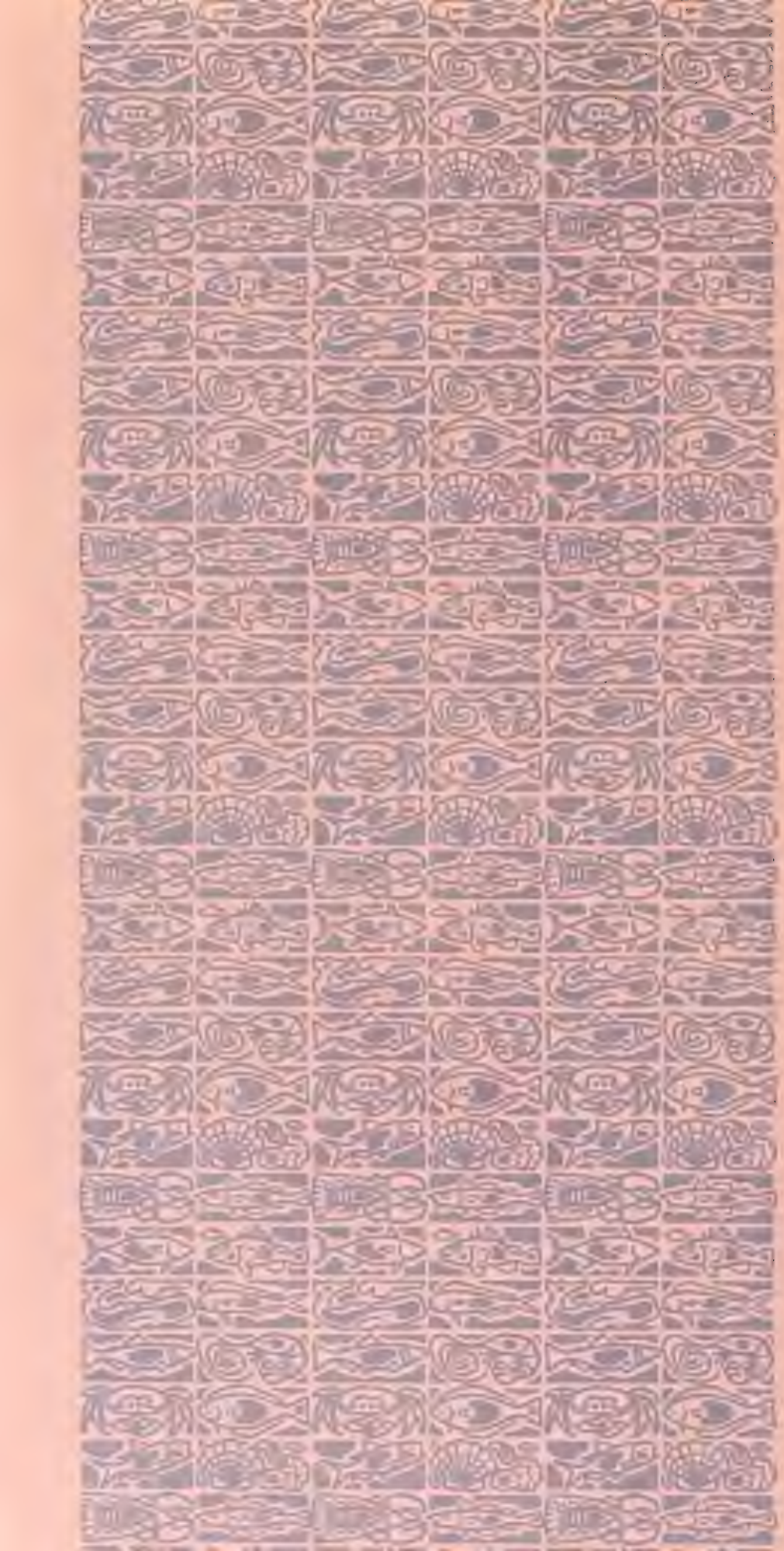

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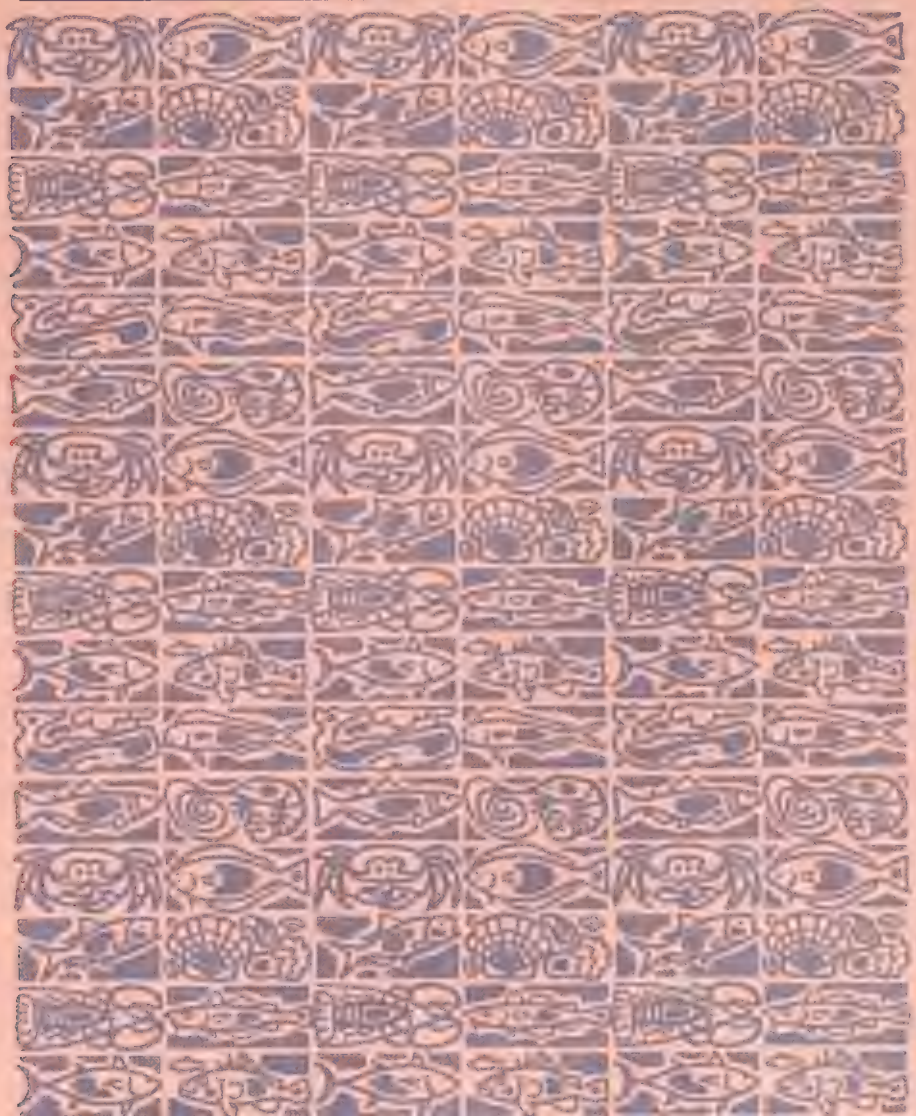

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Awards

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The Publications Advisory Committee of the National Marine Fisheries Service has announced the best publications authored by NMFS scientists and published in the *Fishery Bulletin* for 1987 and 1988 and *Marine Fisheries Review* for 1986 and 1987. Only effective and interpretive articles which significantly contribute to the understanding and knowledge of NMFS mission-related studies are eligible, and the following pages were judged as the best in meeting this requirement.

Fishery Bulletin 1987

Dean W. Ahrenholz, Walter R. Nelson, and Sheryan P. Epperly
Population and fishery characteristics of Atlantic menhaden, *Brevoortia tyrannus*. Fishery Bulletin, U.S. 85:569-600. Dean Ahrenholz and Sheryan Epperly are with the Beaufort Laboratory, Southeast Fisheries Science Center, Beaufort, North Carolina; Walter Nelson is with the Pascagoula Laboratory, Southeast Fisheries Science Center, Pascagoula, Mississippi.

Fishery Bulletin 1988

Edmund S. Hobson and James R. Chess
Trophic relations of the blue rockfish, *Sebastes mystinus*, in a coastal upwelling system off northern California. Fishery Bulletin, U.S. 86:715-743. Both authors are with the Tiburon Laboratory, Southwest Fisheries Science Center, Tiburon, California.

Marine Fisheries Review 1986

Austin B. Williams
Lobsters—Identification, world distribution, and U.S. trade. Marine Fisheries Review 48(2):1-36. The author is with the NMFS Systematics Laboratory, National Museum of Natural History, Washington, D.C.

Marine Fisheries Review 1987

Arthur W. Kendall Jr., and Ann C. Matarese
Biology of eggs, larvae, and epipelagic juveniles of sablefish, *Anoplopoma fimbria*, in relation to their potential use in management. *Marine Fisheries Review* 49(1):1-13. Both authors are with the Resource Assessment & Conservation Engineering Division, Alaska Fisheries Science Center, Seattle, Washington.

John Alan Gulland
1926–1990

We report with sadness the death of John Gulland on June 24, 1990 after a long illness. He is remembered for his work on population dynamics and effects of exploitation on fish stocks, and for his clear insights into the problems of conservation and effective management of fisheries resources.

John Gulland trained at Cambridge as an applied mathematician. Early in his career, he joined the Fisheries Laboratory at Lowestaft. At this time, fisheries in the North Atlantic were rebounding after the hiatus of World War II and it had become clear that scientific management was required. Various international commissions were established for fisheries management, each of which had a scientific committee associated with it. It was not long before Gulland began to play a major role in these committees, insisting on obtaining from each participating country the data needed from their fisheries. It was his careful analysis of these fisheries data and his scientific conclusions that cut through the hypocrisy that was often a mask for political considerations.

In the early sixties, Gulland was loaned to Australia, which in turn loaned him to the Committee of Three, established by the International Whaling Commission (IWC) in 1960 to carry out a scientific assessment of the whale stocks. Gulland quickly became such a valuable member of the group that it was expanded to the Committee of Four. After the Committee made its report, and suggested a substantial cutback in whale quotas, the Food and Agriculture Organization (FAO) of the United Nations was given the task of continuing the studies on status of whale stocks. About this time Gulland transferred to FAO and continued this activity with the IWC for several years.

Also in his new post at FAO, Gulland began to work on the fisheries problems of developing countries around the world. He brought to these problems the same logical mind

and disdain for political solutions that he had earlier shown in his dealings with North Atlantic fisheries. His experience in FAO and a developing association with the College of Fisheries at the University of Washington led him to write several books. These include: *The Fish Resources of the Ocean* (1972), *The Management of Marine Fisheries* (1974, 1977), and *Fish Stock Management* (1977).

Gulland's many accomplishments have been recognized in many ways. He was named Keynote Speaker at the annual meeting of the American Fisheries Society (1977), and, more importantly, he was elected to the Royal Society (1984). He retired from FAO in 1984 and returned to England where he became associated with Imperial College, London. He continued to work on a variety of marine resource problems, as he was doing at the time of his death on 24 June 1990.

While Gulland was an outstanding scientist who developed much of fisheries science and management techniques that are valid today, he was not above "back-of-the-envelope" calculations. He would often use these to demolish opponents who were using apparently sophisticated analyses to obfuscate rather than to clarify. But he also had a delightful lighthearted side to his character. An incident that reflects this side of his personality occurred while he served as an adviser to the Commission for the Conservation of Antarctic Living Marine Resources. The group arranged for him to visit the South Pole in January 1985. While there, he took part in a cricket match on the Beardmore Glacier (the largest glacier in the world). There was no doubt that this was the most southerly cricket match ever played, and as such he often stated that this was the capstone of his career.

Douglas G. Chapman

Erratum

Sturm, Maxwell G. de L., and Premila Salter
Age, growth, and reproduction of the king mackerel *Scomberomorus cavalla* (Cuvier) in Trinidad waters. Fish. Bull., U.S. 88:361–370.

The Abstract, p. 361, should be corrected as follows:

In the fourth sentence, L_∞ should be replaced by L_t in both von Bertalanffy equations, and the male t_0 value should read 1.79 rather than 1.80.

In the fifth sentence, "...peak spawning from October through March..." should read "September through March..."

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Trophic Relations of Juvenile Pacific Salmon off the Oregon and Washington Coast

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Abstract. – Feeding habits of juvenile coho *Oncorhynchus kisutch*, chinook *O. tshawytscha*, chum *O. keta*, and sockeye *O. nerka* salmon were examined from collections taken off the Oregon–Washington coast during the summers of 1980–85. The major prey of both coho and chinook salmon juveniles were larval and juvenile fishes, although a substantial proportion of the diet of coho salmon consisted of invertebrates such as euphausiids, decapod larvae, and hyperiid amphipods. Juvenile chum and sockeye salmon had a more varied diet consisting generally of smaller prey, such as juvenile euphausiids, copepods, amphipods, and chaetognaths. Diet overlap was highest between coho and chinook salmon. Both dietary overlap and diversity varied substantially among cruises and individual collections.

Pronounced seasonal and interannual variations occurred in the utilization of the major prey taxa by coho and chinook salmon which may have been related to highly variable oceanographic conditions prevailing during this period. Areal (latitudinal and cross-shelf) variations were of lesser importance in the diets of juvenile coho and chinook salmon.

Manuscript accepted 29 May 1990.
Fishery Bulletin, U.S. 88:617–636.

Until recently, much of the interannual variability in the survival of Pacific salmon *Oncorhynchus* spp. was believed to be a result of conditions occurring in freshwater. It was surmised that by releasing high and relatively constant numbers of hatchery smolts in freshwater, much of the interannual variation in salmon production could be circumvented. Contrary to this assumption, a number of recent studies have found that a substantial portion of the total natural mortality for most salmon species may occur during estuarine and early marine residence (Parker 1968, 1971; Mathews and Buckley 1976; Bax 1983; Furnell and Brett 1986; Fisher and Pearcy 1988). For coho salmon *O. kisutch* originating from Oregon and Washington rivers, peak mortality appears to happen very early in the ocean, perhaps within the first month, and year-class size appears to be well established by the end of the first summer in the ocean (Pearcy 1988).

We still do not know the exact cause of this early ocean mortality. Annual variability in ocean survival of Oregon–Washington salmon stocks appears to be quite large. Both depensatory environmental factors, such as upwelling (Gunsolus 1978, Nickelson 1986), and compensatory biotic interactions such as competition or predation (Peterman 1982, Peterman and Routledge 1983, McGie 1984) have been implicated in the early ocean mortality of juvenile salmon. In either situation, early ocean feeding may be important, and perhaps critical, to growth and survival of salmonids.

Knowledge of the feeding habits and diet variability of juvenile salmon in the coastal ecosystem off Washington and Oregon is incomplete. Peterson et al. (1982) described the diets of juvenile coho, chinook *O. tshawytscha*, and chum *O. keta* salmon for one month (June 1979) and three different geographical areas off southern Washington and Oregon. Emmett et al. (1986) examined seasonal variations in juvenile coho and chinook salmon feeding habits from three time-periods during 1980, but did not examine geographic variations in any detail. There were substantial within and between-study differences in the food composition of these salmonids, although the relative importance of the geographical and temporal components of the variability could not be assessed because of the different sampling designs of the two studies.

This paper describes the diet composition and feeding relationships of juvenile coho, chinook, chum, and sockeye (*O. nerka*) salmon collected from coastal waters off Washington and Oregon during a series of summer purse-seine collections made from 1980 to 1985. Oceanographic conditions and biological productivity were highly variable during this period, both seasonally and interannually (Fisher and Pearcy 1985, Brodeur and Pearcy 1986), and thus provided a fortuitous situation in which to examine the effects of environmental variability on juvenile salmon feeding habits. In addition to examining the interannual variation in feeding, the broad seasonal and geographic coverage of the sampling permitted more detailed intra-annual and areal resolution than was previously possible. Particular detail will be provided for coho and chinook salmon juveniles, which were the dominant salmonids caught (Pearcy 1984, Pearcy and Fisher In press). Although the importance of other potential sources of variability in the diet, such as those attributable to the time of day and predator size, is recognized, these additional factors are discussed in detail elsewhere (Brodeur and Pearcy 1987, Brodeur In press).

Methods

Collection of stomachs

Juvenile salmon were collected with small-mesh (32 mm stretched), large volume (up to 1 million m^3) herring purse seines (Pearcy and Fisher 1988). Sampling was conducted in known areas of salmon concentration in 1980; in following years, predesignated stations were sampled along parallel transect lines spaced approximately 37 km apart (Fig. 1). Along each transect, stations were located every 9.3 km (5 miles) beginning onshore at the 37-m (20 fm) isobath and continuing out to 56 km from the coast or until no juvenile salmon were caught. Data from a total of 15 cruises have been included in this study, with at least one cruise taking place during every month from May through September (Table 1). June was the most intensely sampled month and was sampled during each of the 6 years of the study.

Most collections were made during daylight or twilight, although several complete diel series were made (Brodeur and Pearcy 1987). Circular, quantitative haul sets were made at most stations, although a small proportion of the fish used in this study were collected from sets which were held open for up to 45 minutes or from non-quantitative sets (Pearcy and Fisher 1988). After pursing the net, the catch was then concentrated in the bunt of the seine, and either dip-netted out from the seine or hauled onboard the stern of the sampling vessel. Total sampling time for most sets was approximately 20 minutes. Ancillary physical (temperature and salinity) and biological (chlorophyll *a* and some zooplankton) data were collected before or after the fish collections. A detailed listing of the station locations and many of the physical and biological measurements are given by Fisher and Pearcy (1985) and Brodeur and Pearcy (1986).

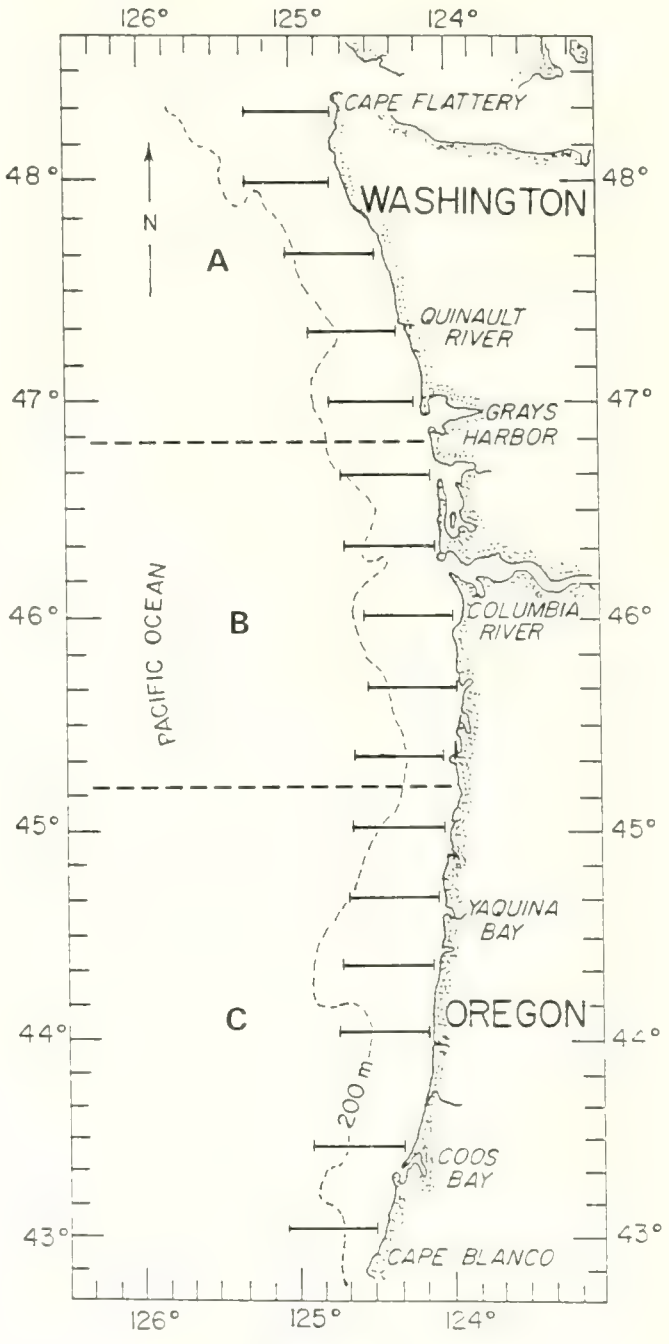

Figure 1

Location of sampling transects and geographic subareas defined in this study.

Table 1

Summary of sampling off Oregon and Washington by cruise from 1980 to 1985. Number of sets includes only quantitative, round hauls taken within 56 km of the coast.

Cruise no.	Year	Dates of cruise	Latitudinal range sampled (North latitude)	Number of sets
1	1980	June 20–28	46°20′–44°30′	33
2	1981	May 16–25	46°35′–44°30′	63
3	1981	June 9–19	46°35′–43°11′	67
4	1981	July 9–19	46°35′–44°25′	71
5	1981	August 8–19	46°35′–43°11′	66
6	1982	May 19–June 2	48°20′–44°00′	62
7	1982	June 7–22	47°20′–44°20′	56
8	1982	Sept. 4–14	47°20′–44°20′	40
9	1983	May 16–27	48°20′–44°20′	57
10	1983	June 9–27	48°20′–43°00′	58
11	1983	Sept. 15–24	48°20′–43°28′	52
12	1984	June 6–20	48°20′–43°28′	66
13	1984	July 19–30	48°00′–44°00′	40
14	1984	Sept. 1–15	48°20′–44°00′	63
15	1985	June 10–25	48°00′–43°27′	78
			Total	865

Once aboard, the juvenile salmon were quickly separated from the rest of the catch and anaesthetized in MS-222 to prevent regurgitation during handling. Each fish was tentatively identified, measured to the nearest mm (fork length), individually labeled, and either preserved whole in formalin after slitting the body cavity (1980 and part of 1981) or frozen whole in a −20°C freezer.

In the laboratory ashore, species identifications were verified and individual wet weights were recorded to the nearest 0.1 g. Stomachs were then removed from a random subsample of up to 10 individuals per species for each collection, with the stipulation that the entire size range of each species represented in the sample be included. Stomachs were individually preserved in a 10% formalin solution and then transferred to a 70% ethanol solution prior to examination. Subyearling and yearling juveniles of each species in their first year in the ocean were distinguished from adult fish using scale analysis (Fisher and Pearcy 1988).

Stomach analysis

Stomachs were opened and the relative fullness was subjectively assessed on a scale from 0 (empty) to 5 (fully distended). The entire stomach contents were blotted on absorbent paper to remove excess moisture and weighed to the nearest 1 mg. The contents were identified under a dissecting microscope to the lowest possible taxonomic level and life-history stage. During this analysis, each prey taxon was assigned a digestion code ranging from 0 (well digested) to 4 (fresh), and a digestion level for the entire stomach was derived from these codes based on the relative proportion by weight of each taxon. Each prey taxon was then enumerated, blotted to remove excess moisture, and weighed to the nearest 1 mg.

Statistical analyses

Three measures were used to determine the importance of each prey taxon to a particular predator: the percent frequency of occurrence in non-empty stomachs (F), the percent of total number of prey organisms (N), and the percent of total weight of prey organisms (W). These measures were combined into a single number, the Index of Relative Importance (IRI = F (N + W)), modified from that described by Pinkas et al. (1971) using weight instead of volume, so that comparisons can easily be made between the relative prey composition of different collections or species. Prey items that were digested or taxa difficult to count, such as gelatinous organisms, were not assigned IRI values. The IRI values were then converted to percent of total IRI for each predator species.

Niche breadth, expressed as the scope of utilization of food resources by each predator species, was calculated using the Shannon-Weaver formula:

$$H'_i = -\sum_{j=1}^{n} P_{ij} (\log_2 P_{ij})$$

where P_{ij} = the proportion by weight of a prey item j in predator i (Petraitis 1979). This index is influenced by both the number of species in the stomachs and the evenness with which they are distributed among the stomachs, and attains a maximum value (H'_{max}) of $\log_2$ (number of prey taxa). The ratio of H' to H'_{max} provides a measure of the evenness with which the resources are distributed among the predators (Pielou 1977).

Diet overlap was calculated among all species for the entire data set and between coho and chinook by cruise or collection where at least 10 stomachs of each species were examined. Schoener's Percent Similarity Index (PSI) was used since it was found to have the most favorable properties within the range of normal overlap values in the absence of prey availability data (Linton et al. 1981, Wallace 1981) where:

$$PSI = [1.0 - 0.5 (\sum | P_{ij} - P_{kj} |)] \times 100$$

where P_{ij} is the proportion by weight of food category

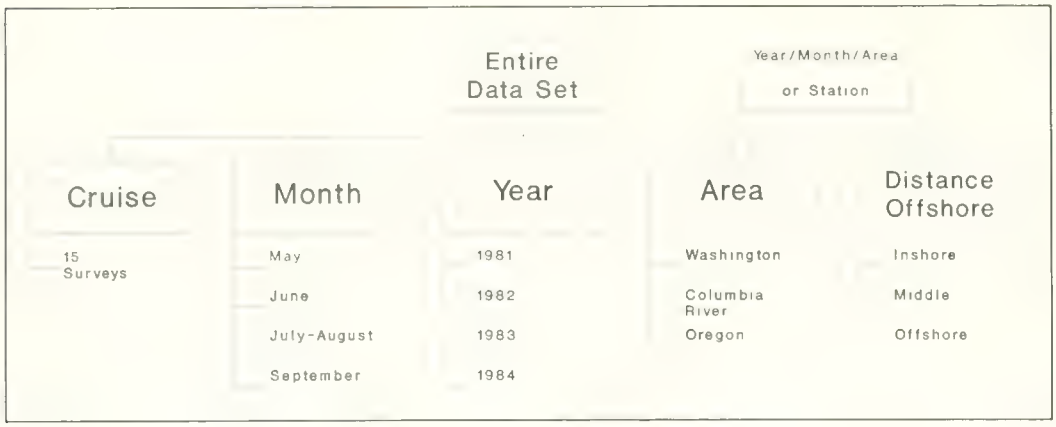

Figure 2
Hierarchy of data groupings used in the analysis of dietary variations in juvenile Pacific salmon.

j in the diet of species i, and P_{hj} is the proportion by weight of food category j in the diet of species h. This index ranges from 0 when two predators have no prey in common to 100 when they have identical diets. Overlap values greater than 60 are generally considered significant. Food availability was considered to be the same for all predators in any one comparison.

The detailed stomach data were then truncated to major taxonomic categories so that general trends in feeding by month, year, and area could be elucidated. Stomach samples of each salmon species were grouped into smaller subsets in a number of different ways to examine diet variability (Fig. 2). The diets of coho and chinook salmon were first examined by cruise so that temporal variability between cruises could be assessed. Data were then grouped by month into four time-periods: May (three cruises), June (six cruises), July–August (three cruises), and September (three cruises). Seasonal changes in diets were then analyzed for these time-periods, regardless of the year or area of collection. Similarly, diets were analyzed by year of collection for those years (1981–84) when multiple cruises exist. North-south geographic variations were examined for each of three subareas within the total sampling area. The collections were stratified latitudinally (Fig. 1) into three areas: (A) north of 46°40′N, (B) between 46°40′N and 45°20′N, and (C) south of 45°20′N (Brodeur et al. 1987a). Food habits were examined for each of these areas for all months and years combined. Finally, diets were examined within each year/month/area subset or by collection so that smaller-scale variations in the food and dietary overlap could be assessed.

Another potential source of geographic variability was that associated with inshore-offshore variations in prey availability and abundance. This source of variation was examined for several cruises where a large number of collections of coho or chinook salmon were obtained far offshore. For these cruises, collections were divided into inner shelf (<18 km from shore), middle shelf (18–37 km), and outer shelf (>37 km) stations. Diets of chum and sockeye salmon were also examined for variation with respect to the different factors when sample sizes were adequate.

The relative importance of the interannual, seasonal, and geographic variations seen in the diets of coho and chinook juveniles was tested by comparing the presence and absence of a particular major prey category using a variance test of binominally distributed data (Snedecor and Cochran 1967) for each factor individually irrespective of the others. When a value exceeded the tabulated 0.05 chi-square percentage, the null hypothesis that the diets were similar was rejected.

Results

Coho salmon

General food habits Juvenile coho salmon had a relatively diverse diet with many different prey categories represented in the stomachs examined for all years combined (Appendix Table 1). A high percentage (95.2%) of the stomachs contained food, and the overall stomach fullness ($\bar{x}$ 3.0) and digestion ($\bar{x}$ 2.3) codes were high indicating that many of the juvenile coho had fed prior to capture.

The primary food groups consumed by juvenile coho salmon were fishes, decapod larvae, amphipods, euphausiids, pteropods, and copepods (Appendix Table 1). Larval and juvenile fishes were the most important prey making up 72% of the total weight and 60% of the total IRI. Rockfishes *Sebastes* spp., northern anchovies *Engraulis mordax*, and Pacific sand lance *Ammodytes hexapterus* were the dominant fish taxa. Although other fish families were represented in the diet, notably the Osmeridae, Cottidae, Hexagrammidae, and Pleuronectidae, each of these families made up less than 1% of the total diet by percent IRI.

Table 2
Food habits by percent weight of major food categories for coho salmon, by cruise, off Oregon and Washington.

	1980	1981				1982			1983			1984			1985
	June	May	June	July	Aug.	May	June	Sept.	May	June	Sept.	June	July	Sept.	June
Prey category															
Fishes	82.8	75.6	73.3	17.6	65.1	75.6	75.6	83.1	73.2	82.7	81.9	83.6	26.1	61.0	82.1
Euphausiids	4.4	2.0	11.0	22.2	31.7	16.0	13.3	2.9	7.3	0.7	10.5	4.9	15.2	17.5	6.3
Decapods	3.5	8.4	11.9	3.5	0.3	6.9	4.2	0.6	12.8	15.6	0.1	10.9	13.2	5.6	6.3
Hyperiids	0.9	0.7	0.4	3.9	1.2	0.8	3.9	5.7	1.5	0.6	3.9	0.1	3.5	13.4	4.8
Pteropods	0.2	10.1	1.6	51.1	0.3	0.3	0.3	6.7	1.6	<0.1	2.1	–	0.1	0.5	<0.1
Copepods	<0.1	0.2	0.3	0.3	0.1	<0.1	<0.1	<0.1	1.3	0.1	<0.1	0.3	0.4	<0.1	<0.1
Insects	<0.1	–	<0.1	0.1	0.1	0.2	0.1	<0.1	0.3	<0.1	<0.1	<0.1	40.0	<0.1	0.1
Cephalopods	6.9	0.6	0.3	–	1.2	–	–	0.9	<0.1	–	1.3	–	0.4	1.0	–
Other*	1.1	0.4	0.8	0.8	<0.1	1.8	1.0	<0.1	0.2	<0.1	0.1	0.1	1.2	<0.1	0.4
Predator characteristics															
No. stomachs	77	245	139	115	94	57	124	144	112	125	102	81	75	61	101
No. empty	1	15	13	3	6	1	4	5	1	7	3	7	7	3	3
Mean length	167.9	153.3	173.7	200.4	231.6	151.9	149.6	247.4	164.7	191.5	270.5	175.7	208.9	275.0	188.4
Length range	81–292	111–238	113–314	92–390	138–386	124–188	120–220	137–410	117–421	125–349	152–420	121–247	144–347	177–366	113–262
Mean no. prey	17.8	26.9	45.3	123.2	38.1	9.1	12.1	97.3	35.8	37.2	61.5	20.7	35.3	80.7	35.3
Mean wt. prey	1.46	0.57	1.15	1.40	2.28	0.59	0.50	2.85	0.91	1.23	5.35	1.16	0.70	0.88	1.54

* Includes polychaetes, chaetognaths, gammarids, isopods, cumaceans, cirripedes, mysids, and gelatinous zooplankton.

Many invertebrate prey also occurred frequently or were important numerically in the diet of juvenile coho salmon, but were much less important than fish by weight (Appendix Table 1). Principal invertebrate prey were *Cancer* crab megalopae, the hyperiid amphipods *Hyperoche medusarum* and *Themisto pacifica*, the euphausiids *Thysanoessa spinifera* and *Euphausia pacifica*, and the pteropod *Limacina helicina*. Numerous other species of decapod larvae and amphipods were eaten, as well as copepods and insects, but were of lesser importance. Juvenile *Loligo* squid were also important prey by weight.

Temporal variations Some between-cruise variability in the weight composition of the major food categories was evident (Table 2). During June 1980, coho salmon consumed mainly fishes, although cephalopods were relatively important compared with other cruises. Except during July, fishes dominated the diet during 1981. Pteropods, mainly *L. helicina*, comprised over one-half the total weight of prey in July 1981. Fishes (mostly *A. hexapterus* and *E. mordax*) and euphausiids (mainly *T. spinifera*) dominated the diet during 1982. During 1983 and 1984, coho salmon juveniles fed more upon decapod larvae than during most other years (Table 2). Several anomalous prey items of more southerly origin appeared in the diet in 1983 and 1984, including the euphausiid *Nyctiphanes simplex*, the pteropod *Euclio pyrimidata*, and the hyperiid amphipod *Vibilia* spp. The greatest number of major prey categories were found during July 1984 when terrestrial insects made up over a third of the biomass found in the coho salmon stomachs. One large lepidopteran, *Choristoneura occidentalis*, comprised greater than 37% of the total prey IRI. The diet during June 1985 resembled that of June 1982 at both the specific and general taxonomic levels.

Based on the percent of IRI for the major prey categories, juvenile coho salmon diets changed somewhat as the summer progressed (Fig. 3). Fishes were the main prey during May, although decapod larvae and pteropods were important numerically. During June, fishes and decapod larvae were the primary prey, with amphipods and euphausiids of relatively minor importance. By July and August, fish consumption decreased substantially, and pteropods and euphausiids were the major taxa consumed. Fishes were again the dominant food in September, but their importance was based mainly on weight because individual fish in the stomachs were comparatively larger. In September, pteropods, euphausiids, and amphipods were important prey numerically.

Geographic variations Diets of juvenile coho salmon in the three geographic areas were similar in that the same major prey categories were represented, despite differences in mean size of salmon among the regions. Fishes, decapod larvae, euphausiids, pteropods, and

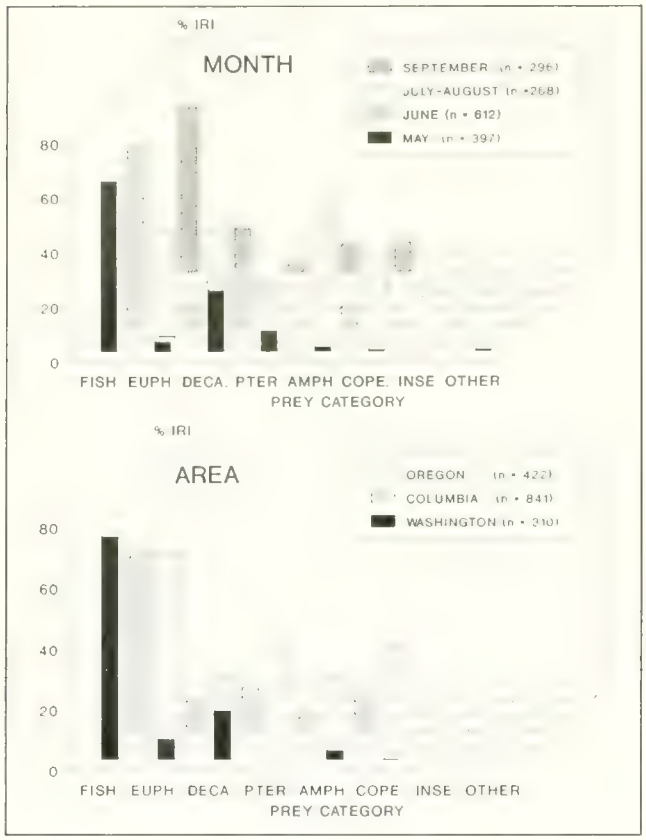

Figure 3

Juvenile coho salmon diets by month and area for the major prey categories as a percent of total IRI. Sample sizes (no. of fish with food) for each subset are given in the legend. All figures include data collected off Washington and Oregon, 1980–85.

amphipods were the dominant prey in each area based on IRI proportions (Fig. 3). The relative proportions of the major prey categories were similar among the regions, although fishes were more important off Washington.

Few differences were observed among the three regions even at the lowest taxonomic levels. *Engraulis mordax* and *Sebastes* spp. were the dominant fish prey by weight in all three regions. The Washington area differed somewhat from the other regions in that *Cancer* larvae were the dominant invertebrate taxa numerically, whereas *L. helicina*, *T. spinifera*, and *H. medusarum* were dominant in the other regions.

Chinook salmon

General food habits Fishes dominated the diet of juvenile chinook salmon, occurring in over 85% of the stomachs that contained food (n = 795), and accounting for almost 87% of the total IRI for all years combined (Appendix Table 1). The overall mean stomach fullness (2.8) and digestion (2.3) states were similar to that of coho. Also resembling the diet of coho salmon, the main fish prey identified were *E. mordax*, *Sebastes* spp., and *A. hexapterus*, but cottid juveniles (*Hemilepidotus spinosus*) were also frequently eaten. Pleuronectid and agonid larvae were more common in the diets of juvenile chinook salmon.

Many invertebrate species were also represented in juvenile chinook salmon diets. The relative importance of the various invertebrate taxa was similar to that found for coho salmon. Decapod larvae, euphausiids, and hyperiid amphipods were the dominant invertebrate groups consumed. The dominant species in these prey categories were *C. oregonensis* megalopae, *T. spinifera*, and *H. medusarum*, respectively (Appendix Table 1). Copepods and mysids were generally more important, and pteropods and insects less important, in comparison with juvenile coho salmon.

Temporal variations Between-cruise variability in the consumption of the major prey taxa was less pronounced for chinook salmon than for coho salmon (Table 3). Fishes comprised 75% or more of the biomass consumed during every cruise, with the exception of July 1981 when euphausiids and pteropods were also major prey. The only other invertebrate taxa to contribute substantially in other cruises were cephalopods (May and June 1981), euphausiids (May 1982 and July 1984) and decapod larvae (May and June 1983). In contrast to the diet of coho salmon, insects were unimportant during July 1984 (Table 3).

Seasonally, the relative IRI proportions of fishes, decapod larvae, and euphausiids were similar for chinook salmon (Fig. 4). The diets contained more major prey categories during July–August when small zooplankton prey (copepods, pteropods, decapod larvae, and hyperiid amphipods) were important numerically. This may be due to the smaller mean size of chinook salmon collected this period; in July–August, there was an influx of subyearling chinook salmon into the sampling area. Fishes were again the dominant prey in September, although hyperiid amphipods remained important numerically.

Geographic variations The feeding patterns of juvenile chinook salmon were fairly consistent by major taxonomic categories among the three regions (Fig. 4). Fishes were the major prey by frequency of occurrence and weight in all three geographic areas, although the dominant species varied somewhat. Off Washington, *A. hexapterus*, *Sebastes* spp., and *H. spinosus* were the main fish prey consumed. *Engraulis mordax* and *H. spinosus* were the dominant prey in the Columbia region, whereas *E. mordax* dominated the diet off Oregon (>65% of the total IRI).

Table 3

Food habits by percent weight of major food categories for chinook salmon, by cruise, off Oregon and Washington.

	1980	1981				1982			1983			1984			1985
	June	May	June	July	Aug.	May	June	Sept.	May	June	Sept.	June	July	Sept.	June
Prey category															
Fishes	92.7	84.5	75.4	38.6	97.3	81.9	94.7	91.9	89.0	80.4	98.2	89.5	75.0	88.5	87.8
Euphausiids	0.1	4.1	0.3	32.7	0.6	13.2	0.4	0.6	1.1	0.1	<0.1	0.1	10.0	6.8	6.3
Decapods	0.4	2.8	8.8	6.9	0.3	3.9	3.1	<0.1	9.4	13.8	0.4	5.2	6.2	2.3	4.9
Hyperiids	—	<0.1	<0.1	3.3	0.5	0.6	<0.1	3.6	<0.1	0.4	0.5	0.2	2.5	1.5	0.3
Pteropods	—	0.1	<0.1	10.6	0.4	0.1	<0.1	—	0.1	<0.1	—	—	—	<0.1	—
Copepods	0.4	<0.1	<0.1	0.4	0.5	<0.1	<0.1	—	<0.1	0.6	<0.1	2.9	5.8	—	<0.1
Insects	—	<0.1	0.8	0.2	<0.1	—	—	0.6	—	—	<0.1	—	—	0.6	<0.1
Cephalopods	—	7.7	14.1	—	—	0.9	—	3.1	0.1	3.6	0.4	1.2	—	0.1	0.3
Other*	6.2	—	0.2	6.9	0.3	<0.1	<0.1	—	<0.1	—	0.5	0.2	0.6	0.1	0.5
Predator characteristics															
No. stomachs	14	63	32	53	32	121	112	10	95	27	89	60	21	37	74
No. empty	0	7	2	6	2	5	2	0	3	2	1	11	2	3	3
Mean length	232.5	181.8	196.5	152.9	165.0	218.9	203.7	322.9	192.6	205.7	220.3	182.2	147.2	215.1	209.9
Length range	189–283	126–290	110–331	87–347	120–347	123–400	119–350	134–435	118–396	124–287	129–325	105–370	109–251	138–412	101–354
Mean no. prey	14.6	27.8	19.0	17.0	37.4	10.8	9.4	12.0	17.1	16.0	13.7	21.9	17.4	12.3	19.2
Mean wt. prey	1.85	1.23	1.47	0.44	0.37	2.44	1.50	1.14	0.99	0.78	3.22	0.98	0.27	0.75	0.85

*Includes polychaetes, chaetognaths, gammarids, isopods, cumaceans, cirripedes, mysids, and gelatinous zooplankton.

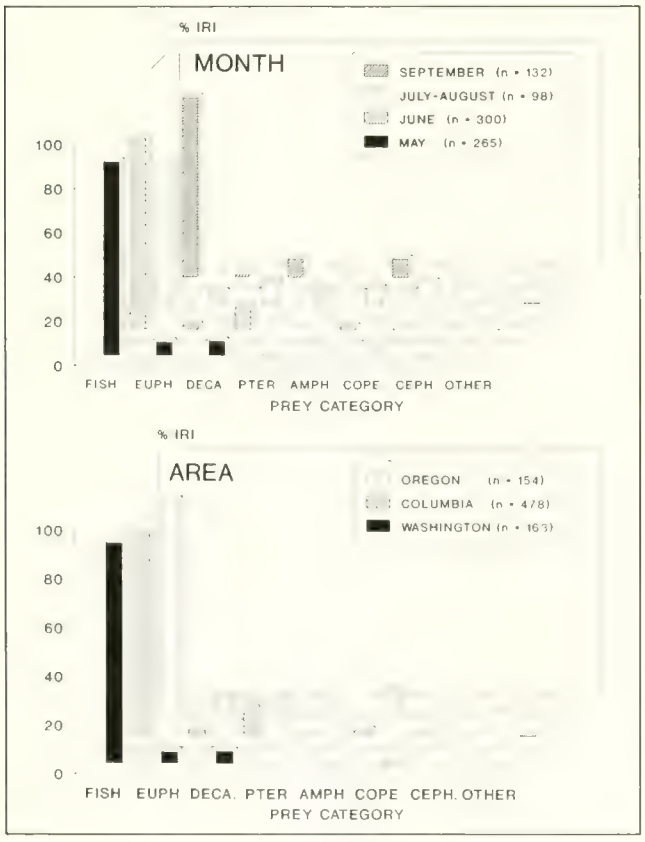

Figure 4

Juvenile chinook salmon diets by month and area for the major prey categories as a percent of total IRI. Sample sizes (no. of fish with food) for each subset are given in the legend. All figures include data collected off Washington and Oregon, 1980–85.

There were few consistent patterns observed among the invertebrate taxa consumed between the different areas (Fig. 4). Hyperiid amphipods were rarely found in chinook salmon stomachs collected off Washington as opposed to the other regions. The large numbers of decapod larvae eaten off the Columbia River were mainly *C. oregonensis* and *C. magister* larvae.

Chum salmon

General food habits Of the 109 chum salmon stomachs examined, 101 (92.6%) contained food; however, overall mean stomach fullness (2.4) and digestion (2.1) were low. The diet was dominated by zooplanktonic crustaceans, particularly euphausiids, calanoid copepods, and hyperiid amphipods (Appendix Table 2). Euphausiids (mostly juvenile *E. pacifica* and *T. spinifera*) accounted for over 54% of the total weight and 47% of the total IRI for all cruises combined. A taxonomically diverse array of hyperiids, copepods, and decapod larvae were also consumed. These taxa frequently occurred in the stomachs and were important numerically, but were of lesser importance gravimetrically. Chaetognaths and larvae and juveniles of several fish species were the dominant non-crustacean prey (Appendix Table 2).

Temporal variations Chum salmon diets varied considerably during the 5 years examined (Table 4). Some

Table 4

Summary of food habits by percent weight of major prey categories for juvenile chum salmon, by year, off Oregon and Washington.

	1981	1982	1983	1984	1985
Prey category					
Fishes	1.1	-	15.4	57.2	24.1
Euphausiids	78.3	60.7	20.5	13.7	33.0
Decapods	<0.1	8.6	1.0	–	2.0
Hyperiids	4.8	7.8	1.0	1.5	0.7
Pteropods	0.8	<0.1	–	–	–
Copepods	6.0	21.4	1.0	3.8	36.6
Chaetognaths	1.9	1.4	60.1	17.5	2.2
Other*	–	<0.1	0.9	6.1	1.3
Predator characteristics					
No. stomachs	24	33	15	8	29
No. empty	2	1	0	1	4
Mean length	190.6	161.6	116.2	165.4	132.2
Length range	108-237	97-223	103-133	126-214	115-155
Mean no. prey	47.4	8.0	78.1	20.1	83.4
Mean wt. prey	0.69	0.04	0.23	0.19	0.22

*Includes polychaetes, ostracods, mysids, insects, and larvaceans.

Table 5

Total number of prey taxa, Shannon-Weaver niche breadth (H′), maximun niche value (H'_{max}), and evenness (E) for each salmon species off Oregon and Washington, for all samples combined.

Species	Total number of prey taxa	H	H	E
Coho salmon	157	4.55	7.29	0.62
Chinook salmon	136	5.06	7.09	0.71
Chum salmon	51	4.35	5.67	0.77
Sockeye salmon	36	2.74	5.17	0.53

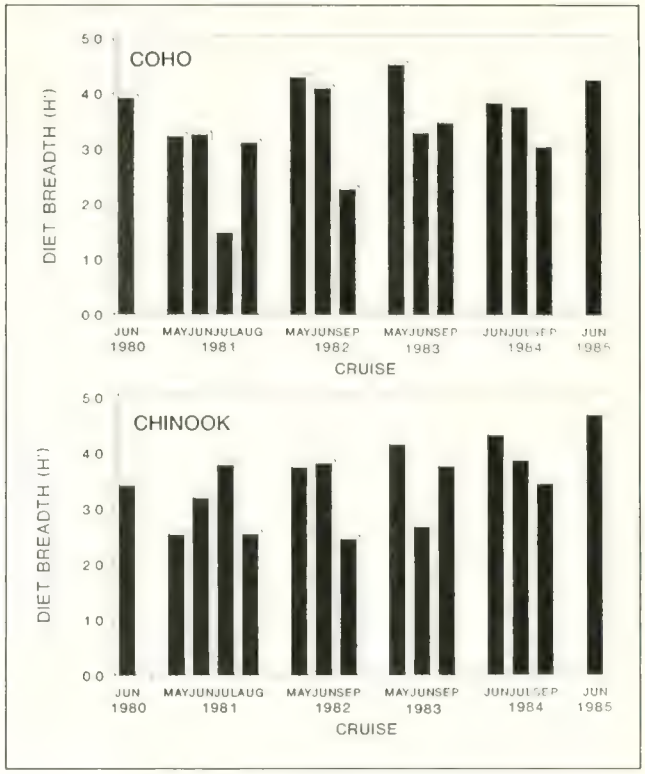

Figure 5

Shannon-Weaver niche breadth (H′) values for juvenile coho and chinook salmon for each cruise period.

of this may be due to the months and areas sampled in different years. Euphausiids were the main food item by weight during 1981 and 1982. Although euphausiids were important during the later years, their contribution to the diet was less compared with chaetognaths, larval fishes, and calanoid copepods.

Sockeye salmon

General food habits The diet of juvenile sockeye salmon was similar to that of chum salmon. Juvenile euphausiids, calanoid copepods, chaetognaths, and fish larvae were consumed by the small number of fish examined (Appendix Table 2). Although a large number of prey taxa were identified, only a few were important. Among these were the euphausiid *T. spinifera* and larval osmerid fishes. Chaetognaths were found in substantial numbers but were well digested and not identifiable to species. The relatively small sample size of sockeye salmon stomachs precluded a detailed analysis of diet variability.

All salmon species

Niche breadth Niche breadths, maximum possible niche breadths, and evenness values are given for each salmon species in Table 5. Chinook salmon had the highest overall diversity of prey taxa (H′ = 5.06), which was consistent with the high numbers of prey taxa found per stomach, and a high evenness ratio. Coho and chum salmon also consumed a diverse array of prey taxa, although coho stomachs frequently contained small numbers of prey items and showed low evenness overall. Chum salmon had a high diversity (H′ = 4.35), despite a substantial amount of unidentified and digested prey, and had the highest evenness (0.77) of all salmon species. The overall prey diversity of sockeye salmon was quite low (H′ = 2.74), which may be due in part to the small sample size and advanced state of digestion (mean digestion code = 2.0) of prey which prevented identification to lower taxonomic levels.

Table 6

Diet overlap by weight among all salmon species off Oregon and Washington, for all cruises combined.

Species	Coho	Chinook	Chum	Sockeye
Coho	–			
Chinook	54			
Chum	26	16	–	
Sockeye	25	24	33	

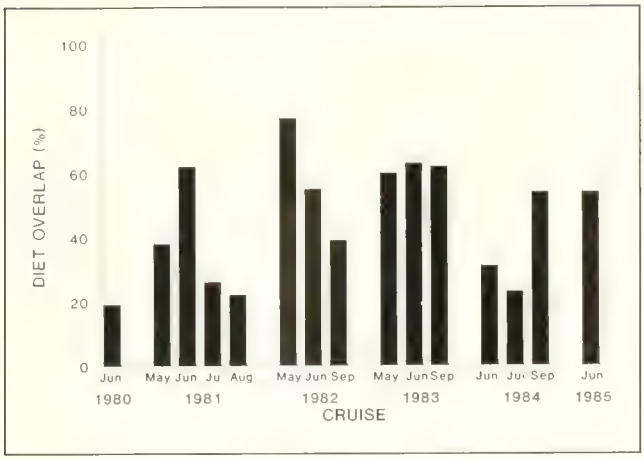

Figure 6

Diet overlap between juvenile coho and chinook salmon for each cruise period, 1980–85.

Table 7

Diet overlap by weight between juvenile coho and chinook salmon for collections off Oregon and Washington from which 10 stomachs of each species were examined. Also shown are the intraspecific overlap values for the same species at adjacent stations collected on the same day.

Date	Location	Distance offshore (km)	PSI Both	PSI Coho	PSI Chinook
1982					
June 1	45°00′, 124°05′	6.1	57		
1	44°41′, 124°24′	18.0	69		
7	47°00′, 124°25′	18.5	53		
8	46°41′, 124°18′	17.4	47	18	40
8	46°41′, 124°29′	31.8	49		
10	46°30′, 124°25′	27.6	45	38	31
10	46°30′, 124°18′	18.3	33		
1983					
Sept. 20	45°40′, 124°03′	8.9	91		
22	45°20′, 124°01′	3.7	62	59	61
22	45°17′, 124°01′	3.7	68		
1984					
June 8	47°00′, 124°25′	18.3	5		
1985					
June 18	46°19′, 124°11′	9.0	56		
25	47°40′, 124°53′	37.3	15		

Prey diversity varied greatly among cruises for juvenile coho (Fig. 5). Generally lower values occurred during 1981, especially in July, when pteropods were very important in the diet. Coho salmon had higher diversity values in 1983 and 1984 than in 1981. Chinook salmon showed many of the same interannual and seasonal trends in prey diversity as coho salmon, except that prey diversity was not appreciably lower in 1981 (Fig. 5).

Dietary overlap Diet overlap by weight among the salmon species for all cruises combined was generally low, with none of the six species pairs showing significant (>60%) overlap (Table 6). The diets of juvenile coho and chinook salmon were most similar (PSI = 54%), reflecting their common foraging on many of the same euphausiid, larval decapod, and fish species. Chum salmon diets showed the least similarity to the other species, which may be a function of the poor digestive state of the stomach contents of this species.

To examine the finer-scale variability in diet similarity between coho and chinook salmon juveniles, diet overlap was calculated for each cruise month (Fig. 6). With the exception of 1983, which showed the highest overall similarity, monthly overlap values were highly variable within years containing more than one cruise. No consistent patterns were observed between years for the same months.

A wide range of diet overlap values was observed for the 13 collections from which 10 stomachs of coho and chinook were analyzed (Table 7). Overlap was highest in the collections from September 1983, due mainly to the common utilization of *E. mordax* and several hyperiid amphipod species. Intermediate overlaps were generally observed during June 1982, resulting mainly from consumption of the same euphausiid species by both predators. There appeared to be no relationship between diet overlap and the inshore-offshore location of the collection. Diet overlap between juvenile coho and chinook at a particular station was generally higher than intraspecific overlap for either species at adjacent stations (Table 7).

Analysis of dietary variations The contingency table analysis for presence or absence of the four most-commonly-occurring major prey categories showed that there were generally highly significant variations ($P \leq 0.001$) in diets of coho and chinook juveniles by

Table 8

Results of the chi-square analysis analyzing each factor independently of the other two for major prey categories of juvenile coho and chinook salmon off Oregon and Washington. Degrees of freedom are in parentheses below each factor.

Prey category	Year† (3)	Month (3)	Area (2)
Coho salmon			
Fishes	75.32***	83.38***	51.54***
Euphausiids	31.19***	106.38***	10.71**
Decapods	39.48***	38.42***	7.80*
Amphipods	74.61***	53.21***	2.79 n.s.
Chinook salmon			
Fishes	68.25***	65.95***	2.51 n.s.
Euphausiids	33.03***	3.15 n.s.	15.48***
Decapods	46.92***	49.15***	5.96 n.s.
Amphipods	14.36**	60.71***	13.15**

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$, n.s. $P > 0.05$
†Tested for 1981-84 only.

Table 9

Results of the chi-square analysis analyzing inshore-offshore variations for major prey categories of juvenile coho and chinook salmon off Oregon and Washington. All significances are at 2 degrees of freedom.

Prey category	Coho salmon		Chinook salmon	
	May 81	June 84	May 82	June 85
Fishes	3.86 n.s.	5.82 n.s.	1.34 n.s.	1.40 n.s.
Euphausiids	3.14 n.s.	2.66 n.s.	1.82 n.s.	9.76**
Decapods	3.83 n.s.	15.07***	9.00*	1.82 n.s.
Amphipods	3.14 n.s.	15.88***	3.23 n.s.	0.41 n.s.

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$, n.s. $P > 0.05$

year and month (Table 8). The only comparison which showed non-significant variation by year or month was the monthly variation in euphausiid occurrences for juvenile chinook salmon. Three prey categories did not show significant variation ($P > 0.05$) when analyzed by area. Comparisons by area showed less significant variation than by year and month for both coho and chinook salmon juveniles for most of the major prey categories (Table 8).

Examination of inshore-offshore variations in major prey composition for four cruises (two each for coho and chinook salmon) showed generally few significant variations by occurrence for the dominant prey categories (Table 9). Although the species and life-history-stage composition of the prey was different in inshore and offshore collections (i.e., more *Sebastes* and *Engraulis* larvae offshore, and more juvenile *Ammodytes*, *Clupea*, and *Hemilepidotus* inshore), all cross-shelf variations in total fish occurrences were not significant ($P > 0.05$). The most significant differences were for decapod larvae, and were due to higher occurrences of *Cancer* spp. megalopae in chinook salmon stomachs inshore in May 1982 and lower occurrences in coho salmon stomachs inshore in June 1984.

Discussion

Overall food habits

This study represents the first detailed description of the diets of several species of sympatric juvenile salmon in coastal marine waters off Washington and Oregon. Despite generally low diet overlaps at the lowest taxonomic levels, there were some similarities in the major prey groups consumed by the salmon species. Juvenile chinook salmon were primarily piscivorous, consuming a variety of larval and juvenile fishes. The diet of coho salmon consisted of both fishes and large zooplanktonic crustaceans, such as euphausiids, crab megalopae, and hyperiid amphipods. Chum and sockeye salmon diets were more diverse than the diets of coho and chinook salmon, with fishes, small crustaceans (euphausiid furcilia and juveniles, crab larvae, and copepods), and chaetognaths being important prey.

Our findings are consistent with what is known of the marine food habits of juvenile salmon off Washington and Oregon and British Columbia. Juvenile chinook salmon tend to be more piscivorous than juvenile coho for the same-sized predator (Healey 1978, 1980; Peterson et al. 1982; Emmett et al. 1986). Coho collected during this study, however, consumed a larger overall mean length of fish prey relative to predator length (Brodeur In press). Juvenile northern anchovy, Pacific sand lance, and rockfishes were the dominant fish species eaten off Washington and Oregon (Peterson et al. 1982, Emmett et al. 1986), and herring and Pacific sand lance were the main fish species consumed off British Columbia (Healey 1978, 1980). Many of these prey fish species tend to be heavily pigmented and are often associated with the neustonic layer in coastal waters (Brodeur et al. 1987b, Shenker 1988, Brodeur 1989).

Macrozooplankton, such as euphausiids, hyperiid amphipods, and crab larvae, are also readily consumed by these juvenile salmon. These macrozooplankton prey may be easily detected due to their large size or darkly-pigmented eyes (Peterson et al. 1982) and occur in large aggregations near the surface (Brodeur et al. 1987b, Shenker 1988). Terrestrial insects, which may be blown

to sea in large numbers during favorable meteorological conditions, can also contribute substantially to the diets of juvenile coho salmon and other salmonids (Brodeur 1989).

Fishes were much less important in the diets of juvenile chum and sockeye salmon; however, the mean and maximum size of the individuals of these species examined in this study were smaller than those of coho and chinook salmon. Juvenile euphausiids were a major component in the diet of chum and sockeye salmon in this study. Peterson et al. (1982) found juvenile euphausiids were a major prey of chum juveniles off Oregon, whereas copepods, larvaceans, and hyperiid amphipods were most important off British Columbia (Manzer 1969; Healey 1978, 1980). Both chum and sockeye consumed a greater number of chaetognaths than coho and chinook, and the importance of these and other soft-bodied prey may be greatly underestimated in most studies because they are probably digested very rapidly in salmon stomachs (Black and Low 1983).

Patterns in dietary variability

The pronounced interannual differences in the diets of most species were expected, even when the collections from same months and areas were examined. Oceanographic conditions varied greatly among the years, with both relatively strong (1982 and 1985), weak (1983 and 1984), and highly variable (1981) upwelling occurring during the study period (Fisher and Pearcy 1988). In addition, a strong El Niño event dominated ocean conditions in coastal waters of the northeast Pacific during the summer months of 1983 and 1984, greatly affecting primary and secondary productivity and fish production (Mysak 1986, Pearcy and Schoener 1987).

Fish prey, as a proportion of the total diet by weight, was generally invariant for the same months among the different years. However, the species composition alternated between coastal and offshore taxa (as identified by Richardson and Pearcy [1977]) depending on the prevalent hydrographic regime in the various years. Several coastal taxa (*Ammodytes hexapterus*, *Clupea harengus pallasi*, *Hemilepidotus spinosus*, and Osmeridae) were more prevalent during strong upwelling years, whereas offshore taxa (*Engraulis mordax*, *Sebastes* spp., *Ronquilus jordani*, and pleuronectid larvae) were eaten more frequently during poor upwelling years. Although ichthyoplankton collections were not made during every year of the stomach sampling, one limited study lends support to our diet observations. In a series of plankton tows along one transect off the central Oregon coast in 1983, Brodeur et al. (1985) found high abundances of offshore fish taxa at inshore stations compared with past studies. The larvae of the northern anchovy were unusually abundant that year, and juvenile anchovy made up the majority of the diet-by-weight of juvenile coho and chinook salmon during September 1983. Osmerid larvae, generally the dominant larvae inshore off Oregon (Richardson and Pearcy 1977), were found in low abundance in both the plankton collections and fish stomachs during 1983.

Several invertebrate taxa showed substantial interannual variation. The pteropod *L. helicina* was one of the most important prey consumed in 1981, but was relatively unimportant in other years. The dominant inshore euphausiid *T. spinifera* was extremely abundant in the stomachs following periods of active upwelling, but was rarely consumed during the El Niño of 1983 and early 1984 (Brodeur 1986). Several species of decapod larvae were present in greater numbers in the diets of all salmon species during 1983 and early 1984. Many other El Niño-related anomalies that were observed in the diet of coho salmon during 1983 were described by Pearcy et al. (1985). The diets of coho salmon during 1984 showed above-average abundances of terrestrial insects, which presumably were blown offshore by anomalous winds during the summer of 1984 (Brodeur 1989).

Strong seasonal variations in feeding habits of juvenile coho and chinook salmon were evident in the years that had multiple cruises over the 5-month sampling period. Some of the variability may have been due to the seasonal increase in the mean size of the salmon, which allowed a greater size range of prey to be consumed later in the summer (Brodeur In press). However, much of the diet variation may have been due to seasonal variations in the abundance of meroplanktonic prey (e.g., decapod and fish larvae). The timing and duration of spawning, larval development, and settlement to benthic juvenile habitat are relatively fixed for most meroplanktonic species (Lough 1975, Richardson and Pearcy 1977, Parrish et al. 1981) such that their seasonal occurrence in the plankton and the diets of juvenile salmon are relatively predictable. Exceptions may occur during anomalous years such as during an El Niño (Bailey and Incze 1985, Brodeur et al. 1985). Several of the major holoplanktonic taxa (e.g., euphausiids, hyperiids, and pteropods) also showed a consistent seasonal succession of developmental stages, but many species were present throughout the summer period (Brodeur 1990).

It was not surprising that geographic (north-south) variations in the diet composition of most salmon species were not as substantial as temporal variations, because most of the prey species are distributed throughout the range of latitudes we sampled. Similar results were found for adult salmonids and nonsalmonid species by Brodeur et al. (1987a). However, oceanographic regimes may be quite variable between

regions (Brodeur and Pearcy 1986), which could result in different feeding conditions for juvenile salmonids within each region. The Columbia River region may be quite different hydrographically and biologically from the upwelling regions off Washington and Oregon due to the presence of a warm, low-salinity plume extending over much of the Columbia River area during the summer. Oceanic species (e.g., *Sebastes* spp., *E. pacifica*) rarely occurred in the stomachs collected from the Columbia region, whereas *E. mordax*, a species whose northern subpopulation spawns within the relatively stable Columbia River plume (Richardson 1980), was generally well represented in salmon stomachs collected in this region.

The relatively minor cross-shelf variations in the major prey taxa consumed by coho and chinook were not expected, considering that many studies have found substantial variations in cross-shelf species distributions (Peterson and Miller 1976, Richardson and Pearcy 1977, Richardson et al. 1980, Shenker 1988). However, the frequency of occurrence of major prey may not be a representative measure of the diet from a particular area. The larvae of many meroplanktonic taxa (e.g., *Sebastes* spp., *Hemilepidotus* spp., and *Cancer* spp.) are generally found offshore and progressively migrate or are transported inshore as they grow prior to settling to an inshore benthic habitat as juveniles (Richardson et al. 1980, Shenker 1988). Euphausiids consumed in our inshore study area were mainly *T. spinifera*, whereas *E. pacifica* were consumed in the offshore area. These euphausiid species have little overlap in distribution (Hebard 1966). Hyperiid amphipods were also represented by an inshore species, *Hyperoche medusarum*, and an offshore species, *T. pacifica* (Lorz and Pearcy 1975). These and other cross-shelf species differences were not detectable when analyzing stomach contents at higher taxonomic levels. However, species-level distinctions may be irrelevant to a foraging predator, if the size, energy content, and behavior of both prey species are similar.

The high prey-diversity and generally high niche-breadth values agree with previous studies which indicate that many of these salmon species are not specialists in their oceanic feeding modes, but rather consume any available prey within the proper size-range. Many of the same geographic, interannual, and seasonal patterns found in the feeding habits of the adult salmonids and pelagic nonsalmonid species (Brodeur et al. 1987a) were found in our study. These similar patterns suggest that the zooplankton and ichthyoplankton population cycles, which are intricately coupled to seasonal production cycles, may be important determinants of the feeding ecology of these salmon species. The ability to switch to alternate prey, when preferred prey are limiting, may be an important factor in the marine survival of salmon.

The high overlaps between coho and chinook juveniles seen for some cruises or individual collections may signify that some competition for prey may be occurring. This interaction could be particularly acute since coho and chinook exhibit a high degree of spatial overlap in their distributions (Pearcy and Fisher In press). This would be conceivable only if prey resources were limiting.

Because of the highly opportunistic feeding mode of most salmonids and the substantial heterogeneity in the physical and biological environment, a large-scale study over extended time-periods may be necessary to adequately describe the feeding dynamics of juvenile salmon. Major departures from the long-term mean oceanographic conditions, as exemplified by an El Niño event, can strongly affect the feeding ecology of many pelagic planktivores. Fulton and LeBrasseur (1985) have hypothesized that a northward shifting of the Subarctic Boundary from its normal position intersecting the coast off Oregon or northern California to well above Vancouver Island, British Columbia, as occurs in El Niño conditions, may expose salmon and other pelagic predators to a novel suite of available prey, with a corresponding downward shift in prey size. Grover and Olla (1987) found that a smaller mean size of copepod was consumed by larval sablefish *Anoplopoma fimbria* during the El Niño year of 1983 than during 1980, a year of relatively normal oceanographic conditions.

Our study also demonstrated anomalies in species composition in the diet during 1983 and early 1984 compared with other years; relatively large northern euphausiids were replaced by much smaller decapod larvae (i.e., Graspidae, Porcellanidae, and Pinnotheridae) and euphausiids (*Nyctiphanes simplex*) of southern origin (Brodeur 1986). Similar interannual shifts were seen in the fish prey-size spectrum consumed by coho and chinook salmon juveniles with generally smaller prey consumed during 1983 and 1984 (Brodeur In press). Consumption of smaller prey must be balanced by consumption of a greater number of prey of equivalent caloric content in order to maintain the similar growth rates seen for coho salmon during the early summers of 1983 and 1984 as non-Niño years (Fisher and Pearcy 1988). Unless prey are more aggregated during El Niño years, smaller prey would require a substantial increase in time and energy spent foraging, relative to time spent avoiding predators. This increased foraging time, at the expense of predator avoidance, may have led to the low coho and chinook salmon survival in the ocean during the El Niño years (Johnson 1988).

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Appendix Table 1

Percent frequency occurrence (F), percent number (N), percent weight (W), and percent index of relative importance (IRI) of food items in juvenile coho and chinook salmon stomachs taken off Oregon and Washington, for all years combined. Numbers in parentheses refer to summaries for major taxonomic groupings.

	Coho salmon				Chinook salmon			
Prey taxa	F	N	W	IRI	F	N	W	IRI
Cnidaria								
Velella velella	0.3	<0.1	<0.1	<0.1	–	–	–	–
Ctenophora								
Unidentified	<0.1	<0.1	<0.1	<0.1	0.5	<0.1	<0.1	<0.1
Siphonophora								
Unidentified	1.0	<0.1	<0.1	<0.1	0.5	<0.1	<0.1	<0.1
Annelida								
Tomopteris septentrionalis	<0.1	<0.1	<0.1	<0.1	–	–	–	–
Tomopteris sp.	0.6	0.1	<0.1	<0.1			–	
Pelagobia sp.	0.1	<0.1	<0.1	<0.1	–	–	–	–
Nereidae	–	–	–	–	0.1	<0.1	0.1	<0.1
Unidentified	0.5	<0.1	<0.1	<0.1	0.1	0.2	<0.1	<0.1
Mollusca								
Gastropoda	(18.4)	(13.4)	(5.9)		(4.1)	(1.3)	(0.3)	
Limacina helicina	16.5	13.0	5.5	10.4	4.0	1.3	0.3	0.3
Euclio pyramidata	1.5	0.3	0.5	<0.1	–	–	–	–
Clio limacina	0.1	0.1	<0.1	<0.1		–	–	
Pteropoda unidentified	0.4	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Cephalopoda	(2.0)	(0.1)	(0.9)		(2.0)	(0.4)	(1.5)	
Loligo opalescens	1.0	0.1	0.8	<0.1	0.7	0.4	1.1	<0.1
Abraliopsis sp.	0.1	<0.1	<0.1	<0.1		–	–	
Gonatidae	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Octopus dofleini	–	–	–	–	0.2	<0.1	0.1	<0.1
Unidentified	0.8	<0.1	0.1	<0.1	0.9	<0.1	0.2	<0.1
Arthropoda								
Copepoda	(9.6)	(2.1)	(0.2)		(8.5)	(2.6)	(0.2)	
Gaussia princeps	–	–	–	–	0.1	<0.1	<0.1	<0.1
Neocalanus cristatus	3.2	0.5	0.1	<0.1	3.8	0.7	0.1	0.1
Neocalanus plumchrus	0.5	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Calanus marshallae	0.5	<0.1	<0.1	<0.1	0.2	0.1	<0.1	<0.1
Calanus pacificus	1.7	0.5	<0.1	<0.1	0.4	1.2	<0.1	0.1
Calanus spp. copepodites	0.6	0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Eucalanus bungii	0.3	0.6	<0.1	<0.1	0.9	0.2	<0.1	<0.1
Metridia pacifica	0.2	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Epilabidocera longipedata	1.6	0.1	<0.1	<0.1	0.6	<0.1	<0.1	<0.1
Euchaeta elongata	0.1	<0.1	<0.1	<0.1		–	–	
Eurytemora americana	0.1	<0.1	<0.1	<0.1			–	–
Candacia bipinnata	0.1	<0.1	<0.1	<0.1	–	–	–	–
Unidentified	3.4	0.2	<0.1	<0.1	2.6	0.3	<0.1	<0.1
Cirripedia								
Unidentified cypris	1.7	0.1	<0.1	<0.1	0.4	<0.1	<0.1	<0.1
Unidentified remains	0.2	<0.1	<0.1	<0.1	–	–	–	–
Mysidacea								
Acanthomysis macropsis	0.1	<0.1	<0.1	<0.1	1.0	<0.1	<0.1	<0.1
Neomysis kadiakensis	0.5	0.1	<0.1	<0.1	1.0	0.1	0.1	<0.1
Mysidopsis californica	0.1	<0.1	<0.1	<0.1	–	–	–	–
Unidentified	0.3	<0.1	<0.1	<0.1	0.5	0.3	<0.1	<0.1
Cumacea								
Eudorella sp.		–	–		0.1	0.2	<0.1	<0.1
Unidentified	<0.1	<0.1	<0.1	<0.1		–		
Isopoda								
Synidotea bicuspida	–				0.1	0.2	<0.1	<0.1
Gnorimosphaeroma oregonensis	–				0.1	<0.1	<0.1	<0.1
Idotea fewkesi	0.2	<0.1	<0.1	<0.1	–		–	

Appendix Table 1 (continued)

Prey taxa	Coho salmon F	Coho salmon N	Coho salmon W	Coho salmon IRI	Chinook salmon F	Chinook salmon N	Chinook salmon W	Chinook salmon IRI
Arthropoda (continued)								
Amphipoda	(42.0)	(22.3)	(3.1)		(20.7)	(9.6)	(0.4)	
Atylus tridens	2.5	1.9	<0.1	0.2	2.5	2.1	<0.1	0.2
Calliopius laeviusculus	0.2	0.3	<0.1	<0.1	–	–	–	–
Cyphocaris challengeri	–	–	–	–	0.1	<0.1	<0.1	<0.1
Unidentified Gammaridea	0.3	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Hyperia medusarum	5.8	1.1	0.2	0.3	2.3	<0.1	0.1	<0.1
Hyperia spinigera	0.1	<0.1	<0.1	<0.1	0.1	0.2	<0.1	<0.1
Hyperoche medusarum	27.6	13.4	1.6	13.9	12.4	6.7	0.2	3.6
Themisto pacifica	13.7	4.2	0.6	2.2	1.9	<0.1	<0.1	<0.1
Primno brevidens	0.5	<0.1	<0.1	<0.1	–	–	–	–
Primno macropa	0.6	<0.1	<0.1	<0.1	1.5	<0.1	<0.1	<0.1
Phronima sedentaria	1.5	0.1	0.1	<0.1	0.9	<0.1	<0.1	<0.1
Paraphronima crassipes	0.3	<0.1	<0.1	<0.1	–	–	–	–
Paraphronima gracilis	0.5	0.1	<0.1	<0.1	–	–	–	–
Vibilia armata	3.6	0.2	<0.1	<0.1	1.0	<0.1	<0.1	<0.1
Vibilia australis	1.3	0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Vibilia propinquus	3.1	0.1	0.1	<0.1	0.2	<0.1	<0.1	<0.1
Vibilia pyripes	0.2	<0.1	<0.1	<0.1	–	–	–	–
Vibilia viatrix	1.7	0.1	0.1	<0.1	0.1	<0.1	<0.1	<0.1
Vibiliidae unidentified	0.8	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Streetsia challengeri	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Oxycephalus clausi	0.2	<0.1	<0.1	<0.1	–	–	–	–
Lestrigonus schizogeniosis	0.1	<0.1	<0.1	<0.1	–	–	–	–
Brachyscelus crusculum	0.5	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Unidentified Hyperiidea	10.6	0.8	0.4	0.4	3.9	0.5	<0.1	0.1
Caprella incisa	0.1	<0.1	<0.1	<0.1	–	–	–	–
Caprella verrucosa	0.1	<0.1	<0.1	<0.1	–	–	–	–
Euphausiacea	(33.7)	(15.6)	(10.2)		(18.2)	(13.0)	(4.7)	
Euphausia pacifica	10.0	1.6	3.9	1.9	2.8	0.8	0.8	0.2
Nematoscelis difficilis	0.2	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Thysanoessa spinifera	19.5	11.6	5.1	11.0	11.1	10.3	3.5	6.4
Nyctiphanes simplex	3.0	0.4	0.2	0.1	1.6	0.1	<0.1	<0.1
Unidentified furcilia	1.3	1.0	<0.1	<0.1	0.6	<0.1	<0.1	<0.1
Unidentified	11.8	1.0	1.0	0.8	5.5	1.7	0.3	0.5
Decapoda	(45.1)	(28.2)	(4.8)		(35.0)	(29.1)	(3.3)	
Hippolyte clarki	0.1	<0.1	<0.1	<0.1	–	–	–	–
Hippolytidae unidentified	0.2	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Pandalus jordani	–	–	–	–	2.3	0.4	0.1	<0.1
Pandalus spp. zoea	0.3	<0.1	<0.1	<0.1	1.6	1.4	<0.1	0.1
Crangon spp. zoea	3.1	1.0	0.1	0.1	5.2	1.1	0.1	0.3
Natantia unidentified	0.5	0.1	<0.1	<0.1	0.5	<0.1	<0.1	<0.1
Callianassa sp. zoea	0.6	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Upogebia sp. zoea	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Emerita analoga	0.2	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Pagurus granosimanus	0.1	<0.1	<0.1	<0.1	–	–	–	–
Pagurus spp. zoea	0.9	<0.1	<0.1	<0.1	0.6	<0.1	<0.1	<0.1
Pagurus spp. megalopae	4.4	1.0	0.1	0.2	2.6	2.4	<0.1	0.3
Petrolithes cinctipes	0.2	<0.1	<0.1	<0.1	–	–	–	–
Petrolithes eriomerus	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Pachycheles pubescens	0.6	<0.1	<0.1	<0.1	0.7	0.2	<0.1	<0.1
Pachycheles rudis	0.5	0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Pachycheles sp. zoea	0.2	<0.1	<0.1	<0.1	0.4	0.1	<0.1	<0.1
Porcellanidae zoea	1.4	0.1	<0.1	<0.1	0.6	0.2	<0.1	<0.1
Porcellanidae megalopae	2.5	0.4	<0.1	<0.1	2.6	0.7	<0.1	0.3
Oregonia gracilis	0.5	<0.1	<0.1	<0.1	0.2	0.2	<0.1	<0.1
Chionoecetes tanneri	0.2	<0.1	<0.1	<0.1	0.6	<0.1	<0.1	<0.1
Pugettia producta zoea	3.2	0.1	<0.1	<0.1	3.1	0.3	<0.1	<0.1

Appendix Table 1 (continued)

Prey taxa	Coho salmon F	Coho salmon N	Coho salmon W	Coho salmon IRI	Chinook salmon F	Chinook salmon N	Chinook salmon W	Chinook salmon IRI
Arthropoda (continued)								
Decapoda (continued)								
Cancer antennarius megalopae	3.6	1.0	<0.1	0.1	2.5	1.3	0.3	0.2
Cancer magister megalopae	8.0	1.1	1.0	0.6	6.0	2.5	1.4	1.0
Cancer oregonensis megalopae	24.2	13.2	2.2	12.5	13.8	8.0	0.6	5.0
Cancer spp. zoea	8.6	5.5	0.3	1.7	1.9	0.6	<0.1	<0.1
Cancer spp. megalopae	4.1	0.4	0.2	0.1	3.3	0.3	0.2	0.1
Fabia subquadrata	0.8	0.1	<0.1	<0.1	1.1	3.3	0.1	0.2
Pinnixia sp. megalopae	0.2	<0.1	<0.1	<0.1	–	–	–	–
Pinnotheridae zoea	5.7	2.7	0.3	0.6	4.0	2.7	0.1	0.5
Pinnotheridae megalopae	2.0	0.3	0.1	<0.1	3.9	2.0	0.1	0.3
Lophopanopeus bellus	2.9	0.4	<0.1	<0.1	0.7	0.1	<0.1	<0.1
Pachygraspus crassipes	0.1	<0.1	<0.1	<0.1	–	–	–	–
Hemigraspus oregonensis	0.2	<0.1	<0.1	<0.1	–	–	–	–
Unidentified larvae	3.6	0.1	<0.1	<0.1	2.6	0.7	0.1	0.1
Unidentified Crustacea	3.2	<0.1	0.2	<0.1	1.1	<0.1	<0.1	<0.1
Insecta	(6.9)	(1.4)	(0.9)		(3.1)	(0.6)	(0.1)	
Psocoptera	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Hemiptera	0.2	<0.1	<0.1	<0.1	–	–	–	–
Cicadellidae	–	–	–	–	0.1	<0.1	<0.1	<0.1
Aphididae	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Homoptera	0.2	<0.1	<0.1	<0.1	–	–	–	–
Coccinellidae	0.1	<0.1	<0.1	<0.1	–	–	–	–
Coleoptera	0.1	<0.1	<0.1	<0.1	–	–	–	–
Hemerobiidae	0.9	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Neuroptera	0.2	<0.1	<0.1	<0.1	–	–	–	–
Choristoneura occidentalis	1.3	0.4	0.8	0.1	–	–	–	–
Geometridae	0.1	<0.1	<0.1	<0.1	–	–	–	–
Lepidoptera	0.4	0.1	<0.1	<0.1	–	–	–	–
Nematocera	0.5	<0.1	<0.1	<0.1	–	–	–	–
Brachycera	0.6	<0.1	<0.1	<0.1	0.4	<0.1	<0.1	<0.1
Chironomid larvae	–	–	–	–	0.1	0.1	<0.1	<0.1
Diptera	0.5	<0.1	<0.1	<0.1	0.2	0.2	<0.1	<0.1
Formicidae	–	–	–	–	0.1	<0.1	<0.1	<0.1
Hymenoptera	0.1	0.1	<0.1	<0.1	0.1	0.2	<0.1	<0.1
Unidentified	4.1	0.7	0.1	0.1	2.4	0.1	<0.1	<0.1
Chaetognatha								
Eukhronia hamata	–	–	–	–	0.1	<0.1	<0.1	<0.1
Sagitta elegans	0.3	0.6	<0.1	<0.1	–	–	–	–
Unidentified	1.2	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Salpidae								
Unidentified	0.4	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Chordata								
Osteichthyes	(66.7)	(15.2)	(72.0)		(85.3)	(42.1)	(88.3)	
Clupea harengus pallasi	3.4	0.1	2.5	0.3	6.3	0.3	1.8	0.5
Engraulis mordax	7.4	0.4	23.3	5.9	12.2	2.0	34.9	18.9
Allosmerus elongatus	0.2	<0.1	0.7	<0.1	0.9	<0.1	2.0	0.1
Spirinchus starksi	–	–	–	–	0.1	<0.1	0.4	<0.1
Osmeridae unidentified	3.4	0.7	1.3	0.2	5.8	0.5	2.9	0.8
Myctophidae unidentified	0.2	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Gadus macrocephalus	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Microgadus proximus	1.7	0.1	1.6	0.1	1.8	0.7	0.6	0.1
Sebastes jordani	0.2	<0.1	0.3	<0.1	0.2	<0.1	0.3	<0.1
Sebastes spp.	14.7	2.6	13.0	7.7	11.7	2.9	8.4	5.5
Hexagrammos decagrammus	0.1	<0.1	0.1	<0.1	0.1	<0.1	<0.1	<0.1
Hexagrammos spp.	0.3	<0.1	0.3	<0.1	–	–	–	–
Ophiodon elongatus	0.5	<0.1	0.2	<0.1	0.6	<0.1	0.1	<0.1
Hexagrammidae unidentified	1.1	0.1	0.9	<0.1	0.4	<0.1	0.1	<0.1

Appendix Table 1 (continued)

Prey taxa	Coho salmon F	Coho salmon N	Coho salmon W	Coho salmon IRI	Chinook salmon F	Chinook salmon N	Chinook salmon W	Chinook salmon IRI
Chordata (continued)								
Osteichthyes (continued)								
Agonopsis vulsa	–	–	–	–	0.1	<0.1	<0.1	<0.1
Odontopyxis trispinosa	–	–	–	–	1.5	0.2	<0.1	<0.1
Stellerina xyosterna	–	–	–	–	0.1	<0.1	<0.1	<0.1
Agonidae unidentified	0.1	0.1	<0.1	<0.1	0.9	<0.1	<0.1	<0.1
Cyclopteridae unidentified	0.1	0.1	<0.1	<0.1	0.6	<0.1	0.1	<0.1
Artedius fenestralis	0.1	0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Artedius harringtoni	–	–	–	–	0.6	<0.1	<0.1	<0.1
Artedius meanyi	0.1	<0.1	<0.1	<0.1	1.0	<0.1	<0.1	<0.1
Hemilepidotus spinosus	5.8	0.2	2.2	0.5	14.0	0.8	6.8	4.5
Radulinus asprellus	0.1	<0.1	<0.1	<0.1	0.5	0.2	<0.1	<0.1
Scorpaenichthys marmoratus	0.8	0.1	0.1	<0.1	0.1	<0.1	<0.1	<0.1
Chitonotus pugetensis	0.1	<0.1	<0.1	<0.1	0.2	0.2	<0.1	<0.1
Cottidae unidentified	1.3	<0.1	0.2	<0.1	4.1	3.5	0.4	0.7
Ammodytes hexapterus	9.5	2.7	4.4	2.3	13.7	4.4	4.3	5.1
Pholidae unidentified	0.1	0.1	<0.1	<0.1	–	–	–	–
Ronquilus jordani	1.6	0.8	0.6	0.1	2.5	4.5	0.4	0.5
Stichaeidae unidentified	0.1	<0.1	<0.1	<0.1	–	–	–	–
Coryphopterus nicholsi	0.1	<0.1	<0.1	<0.1	–	–	–	–
Citharichthys sordidus	0.1	<0.1	<0.1	<0.1	0.4	<0.1	0.1	<0.1
Citharichthys stigmaeus	0.2	<0.1	0.1	<0.1	1.0	<0.1	0.7	<0.1
Atherestes stomias	–	–	–	–	1.0	2.8	0.5	0.1
Eopsetta jordani	–	–	–	–	0.1	<0.1	<0.1	<0.1
Glyptocephalus zachirus	0.4	<0.1	<0.1	<0.1	1.0	<0.1	0.3	<0.1
Hippoglossoides elassodon	–	–	–	–	0.1	<0.1	<0.1	<0.1
Isopsetta isolepis	0.5	<0.1	<0.1	<0.1	3.6	0.2	0.6	0.1
Lepidopsetta bilineata	–	–	–	–	0.1	<0.1	<0.1	<0.1
Lyopsetta exilis	–	–	–	–	0.6	<0.1	0.1	<0.1
Parophrys vetulus	0.4	<0.1	0.1	<0.1	3.3	0.1	0.4	0.1
Psettichthys melanostictus	1.5	0.1	0.5	<0.1	6.7	1.6	1.9	1.0
Pleuronectidae larvae	1.6	<0.1	0.3	<0.1	7.7	0.4	1.1	0.5
Unidentified larvae	8.9	1.3	1.1	0.7	18.7	5.1	3.5	6.8
Unidentified juveniles	4.4	1.7	2.9	0.7	6.2	2.5	4.8	1.9
Unidentified remains	38.0	3.4	14.5	22.9	41.5	8.3	10.2	32.3
Plant material	3.0	0.4	0.2	0.1	1.3	<0.1	<0.1	<0.1
Unidentified material	16.9	0.2	1.2	0.8	9.1	0.1	0.7	0.3
Number of stomachs examined		1652				844		
Number of empty stomachs		79				49		
Mean fork length (mm)		193.80				200.47		
Fork length range (mm)		81–421				81–435		

Appendix Table 2

Percent frequency occurrence (F), percent number (N), percent weight (W), and percent index of relative importance (IRI) of food items in juvenile chum and sockeye salmon stomachs taken off Oregon and Washington, for all years combined. Numbers in parentheses refer to summaries for major taxonomic groupings.

	Chum salmon				Sockeye salmon			
Prey taxa	F	N	W	IRI	F	N	W	IRI
Cnidaria								
Velella velella	1.0	<0.1	0.1	<0.1	–	–	–	–
Siphonophora								
Unidentified	2.0	0.2	0.1	<0.1	–	–	–	–
Annelida								
Tomopteris spp.	–	–	–	–	16.7	0.3	2.2	1.0
Unidentified	2.0	0.3	<0.1	<0.1	–	–	–	–
Mollusca								
Gastropoda								
Limacina helicina	3.0	0.1	0.5	0.1	16.7	1.5	2.5	1.7
Arthropoda								
Ostracoda								
Unidentified	1.0	<0.1	<0.1	<0.1	–	–	–	–
Copepoda	(49.0)	(39.2)	(11.5)		(46.7)	(11.0)	(5.1)	
Calanus marshallae	4.9	0.1	0.3	0.1	3.3	<0.1	0.1	<0.1
Calanus pacificus	12.9	7.4	3.1	4.7	3.3	7.6	2.1	0.8
Calanus spp. copepodites	3.0	1.0	0.4	0.1	3.3	<0.1	0.1	<0.1
Neocalanus cristatus	10.9	2.3	1.8	1.6	10.0	0.1	0.3	0.1
Neocalanus plumchrus	7.9	0.6	0.5	0.3	20.0	1.3	0.6	1.0
Eucalanus bungii	13.9	17.0	3.8	10.0	–	–	–	–
Epilabidocera longipedata	1.0	0.8	0.1	<0.1	6.7	0.3	0.2	0.1
Unidentified	20.8	10.3	1.9	8.8	26.7	1.6	1.5	2.0
Cirripedia								
Unidentified cypris	3.0	<0.1	0.1	<0.1	–	–	–	–
Mysidacea								
Acanthomysis macropsis	1.0	0.3	0.1	<0.1	–	–	–	–
Amphipoda	(46.1)	(5.8)	(7.8)		(46.7)	(2.7)	(3.6)	
Hyperia medusarum	1.0	0.6	<0.1	<0.1	–	–	–	–
Hyperoche medusarum	27.7	2.4	3.1	5.3	36.7	1.4	2.0	3.0
Themisto pacifica	7.9	2.3	0.3	0.7	13.3	0.4	0.3	0.2
Primno macropa	1.0	0.3	<0.1	<0.1	–	–	–	–
Vibilia armata	1.0	<0.1	0.1	<0.1	–	–	–	–
Vibilia australis	–	–	–	–	3.3	0.2	0.1	<0.1
Vibilia viatrix	1.0	<0.1	0.1	<0.1	–	–	–	–
Unidentified Hyperiidea	14.8	0.2	0.8	0.5	23.3	0.7	0.9	0.9
Euphausiacea	(49.0)	(15.7)	(51.1)		(63.3)	(46.2)	(15.1)	
Euphausia pacifica	19.8	3.2	40.8	30.3	20.0	0.4	5.4	2.8
Thysanoessa spinifera	20.8	10.4	7.1	12.7	26.7	44.6	4.2	31.7
Unidentified furcilia	7.9	0.6	0.3	0.3	6.7	0.6	0.3	0.1
Unidentified remains	14.8	1.5	5.9	3.9	33.3	0.5	3.8	3.5
Decapoda	(22.5)	(12.5)	(1.3)		(25.0)	(4.9)	(4.6)	
Hippolytidae zoea	2.0	0.9	0.1	0.1	–	–	–	–
Natantia larvae	3.0	0.1	0.1	<0.1	3.3	<0.1	0.1	<0.1
Pagurus spp. megalopae	–	–	–	–	3.3	0.3	0.3	<0.1
Pugettia producta zoea	6.9	1.2	0.2	0.3	3.3	0.4	0.1	<0.1
Cancer antennarius meg.	1.0	0.6	<0.1	<0.1	3.3	<0.1	0.1	<0.1
Cancer magister meg.	1.0	<0.1	<0.1	<0.1	–	–	–	–
Cancer oregonensis meg	5.9	3.7	0.3	0.8	–	–	–	–
Cancer spp. zoea	7.9	5.6	0.5	1.6	3.3	<0.1	0.1	<0.1
Pachycheles pubescens	–	–	–	–	3.3	1.1	1.0	0.2
Pachycheles rudis	–	–	–	–	3.3	1.0	0.1	<0.1
Porcellanid zoea	–	–	–	–	3.3	0.1	0.1	<0.1
Lophopanopeus bellus	–	–	–	–	3.3	0.1	0.1	<0.1
Pinnotherid megalopae	1.0	0.6	<0.1	<0.1	3.3	0.5	0.5	0.1
Hemigraspas oregonensis	–	–	–	–	3.3	1.1	0.5	0.1
Unidentified larvae	1.0	<0.1	<0.1	<0.1	10.0	0.2	0.4	0.1

Appendix Table 2 (continued)

Prey taxa	Chum salmon F	Chum salmon N	Chum salmon W	Chum salmon IRI	Sockeye salmon F	Sockeye salmon N	Sockeye salmon W	Sockeye salmon IRI
Arthropoda (continued)								
Crustacean remains	11.9	0.1	9.5	4.0	10.0	0.1	1.2	0.3
Insecta								
Diptera	1.0	<0.1	<0.1	<0.1	–	–	–	–
Unidentified	3.0	<0.1	<0.1	<0.1	–	–	–	–
Chaetognatha								
Sagitta elegans	5.9	2.8	2.8	1.2	–	–	–	–
Unidentified	18.8	5.0	5.3	6.8	26.7	18.0	7.5	16.6
Chordata								
Larvacea								
Oikopleura sp.	2.0	2.4	0.4	0.2	–	–	–	–
Osteichthys	(30.4)	(15.0)	(10.4)		(56.7)	(16.2)	(58.2)	
Clupea harengus pallasi	–	–	–	–	3.3	0.2	3.1	0.3
Engraulis mordax	4.9	0.3	1.8	0.4	6.7	0.2	0.2	0.1
Osmeridae	2.0	0.6	0.6	0.1	20.0	1.1	29.0	14.7
Scorpaenichthys marmoratus	1.0	<0.1	<0.1	<0.1	–	–	–	–
Chitonotus pugetensis	1.0	0.3	0.1	<0.1	–	–	–	–
Cottidae	1.0	0.3	<0.1	<0.1	–	–	–	–
Ammodytes hexapterus	2.0	0.9	1.1	0.1	–	–	–	–
Romaulus jordani	6.9	5.2	1.6	1.6	–	–	–	–
Unidentified larvae	7.9	3.2	1.3	1.2	16.7	14.1	9.3	9.5
Unidentified juveniles	1.0	1.4	0.3	1.0	–	–	–	–
Unidentified remains	10.9	2.9	2.1	1.9	13.3	0.5	11.3	3.8
Number of stomachs examined		109				32		
Number of empty stomachs		8				2		
Mean fork length (mm)		154.8				129.8		
Fork length range (mm)		97–237				104–149		

Abstract.– We compared rate of formation of scale circuli and spacing between circuli with fish growth rate and scale growth rate in three groups of young coho salmon *Oncorhynchus kisutch*): (1) smolts held in saltwater tanks, (2) tagged precocious males (jacks) returning to a release facility after only 3 or 4 months in the ocean in two different years, and (3) tagged juvenile coho salmon caught in the ocean. Rate of formation of scale circuli was significantly and positively correlated with fish growth rate and with scale growth rate in all groups. However, rate of circulus formation at a given growth rate was lower for large jacks than for the smaller and younger fish held in saltwater tanks, suggesting that rate of circulus formation is negatively related to size or age of fish as well as positively related to growth rate. Spacing of circuli was also significantly and positively correlated with fish growth rate in all but one group of returning jacks, and with scale growth rate in all groups. The relationship between circulus spacing and fish growth rate varied among groups, partly because the relationships between scale-radius and fish length and between rate of circulus formation and fish growth rate also varied among groups. Scale circulus spacing could be used to compare growth rates between groups of juvenile coho salmon that are of similar size and age and that have a common relationship between scale radius and fish length.

Spacing of Scale Circuli versus Growth Rate in Young Coho Salmon

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Spacing of scale ridges (circuli) is a potentially valuable tool for comparing growth rates of fish where other data are not available. Scale circulus spacing has been found to be positively correlated with fish growth rate in several species of fishes (Doyle et al. 1987; Matricia et al. 1989; Glenn and Mathias 1985; Bhatia 1932; Bilton 1971a, 1975). Use of scales for studying growth has distinct advantages over other methods, such as the spacing of daily rings in otoliths, since scales can be easily obtained without killing the fish and are more quickly prepared and read.

Spacing of scale circuli is determined by both the rate at which circuli are formed and the rate of growth of the scale. Whether scale circulus spacing can be used to estimate fish growth rate depends on whether scale growth and circulus deposition rate are related to fish growth rate in a consistent, predictable manner. To determine the usefulness of circulus spacing for estimating growth rate of juvenile coho salmon, we investigated the relationships between scale radius and fish length, between rate of circulus formation and fish and scale growth rates, and between circulus spacing and fish and scale growth rates in three groups of marked young coho salmon: (1) subyearling (age 0) smolts held in saltwater tanks, (2) yearling (age 1.0)* fish returning as jacks to a coastal hatchery after 3 or 4 months in the ocean in two different years, and (3) marked juvenile coho salmon (age 0.0 and age 1.0) caught in the ocean within 2–4 months of entering the ocean. Our purpose was to develop a method for comparing growth rates of unmarked juvenile coho salmon caught in the ocean in different years (see Fisher and Pearcy 1988).

Methods

Coho smolts held in saltwater tanks

Coho smolts (age 0) were collected from one of the raceways at Oregon Aqua Foods, Inc's. Yaquina Bay, Oregon, release facility and transferred to the Hatfield Marine Science Center in July 1982. About 40 fish were placed in each of seven 1.5-m diameter fiberglass tanks. A constant flow of sea water was maintained to each tank. Daily food rations were varied between tanks from 0.6 to 3.0% of total salmon biomass in order to produce a wide range of fish growth rates. Fish in five tanks were fed Oregon Moist Pellet, while those in two others were fed thawed frozen euphausiids. Water temperature during the experiment was variable, ranging from approximately 11° to 17°C.

During 22–24 July, all the fish were anesthetized with MS-222, measured

* Age designation follows Koo (1962) and Godfrey et al. (1975), where the number to the left of the decimal indicates the number of winters spent in freshwater, and the number to the right of the decimal the number of winters spent in saltwater.

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Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Fork length (FL, mm) vs. scale radius (SR, mm at 88×): Correlation coefficients (r) and geometric mean regressions (GM, Ricker 1973) for age-0 fish held in saltwater tanks (A), for age-1.0 jacks returning to Anadromous, Inc. in 1983 (B) and 1985 (C), and for juvenile coho (ages 0.0 and 1.0) caught in the ocean 1981–84 (D).

Group	n	r	GM regression
A	171	0.96	FL = 1.69 (SR) + 18.54
B	64	0.78	FL = 1.59 (SR) + 65.80
C	99	0.83	FL = 1.99 (SR) + 43.05
D	34	0.96	FL = 2.13 (SR) – 20.64

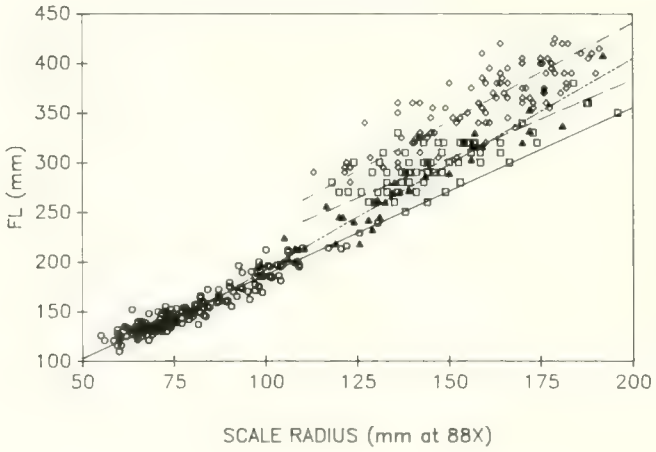

Figure 1

Fork length vs. scale radius scattergrams and GM regression lines for age-0 smolts held in saltwater tanks (○, —), for age-1.0 CWT jacks returning to Coos Bay in 1983 (□, — —) and 1985 (◇, – –), and CWT juvenile fish caught in the ocean (▲, – · · –).

to the nearest mm fork length (FL), and a scale sample taken from the preferred area (Clutter and Whitesel 1956). Each fish was also marked with a unique combination of color spots above the anal fin by injecting acrylic paint under the surface of the skin (Lotrich and Meridith 1974).

Fish were fed for 63–66 days. At the end of the period fish were again anesthetized, measured and weighed, and new scale samples were taken from the preferred area, although sometimes on the other side of the fish. Good scale samples were obtained from 80 fish at the beginning and end of the experiment. Mean fish lengths at the beginning and end of this 63–66 day period were 135 mm FL (SD 8.7, range 110–155 mm) and 171 mm FL (SD 24.5, range 125–229 mm), respectively. Acetate impressions were made of the scales. All scale measurements were made at a magnification of 88× along the axis 20° ventrad of the posterior-anterior axis of the scale.

Scales from each fish taken at the beginning and end of the experiment were compared to determine the spacing and number of circuli laid down during the intervening growth period. Mean circulus spacing during the growth period was calculated as $(SR_2 - SR_1)/n$, where SR_2 is the radius to last scale circulus, SR_1 is the radius to last circulus before the growth period as determined by comparison with the initial scale sample, and n is the number of new circuli formed during the growth period. Rate of circulus formation for each fish was also determined (n/d, where d is the duration of the experiment in days).

Linear growth rate was calculated for each fish as $(FL_2 - FL_1)/d$, where FL_1 and FL_2 are the lengths (mm) at the beginning and end of the experiment, respectively. Scale growth rate was also calculated as $(SR_{tot} - SR_1)/d$, where SR_{tot} is the total scale radius.

Returning jacks

Fork length was measured and scale samples taken from the preferred area of 64 and 99 coded-wire tagged (CWT) jacks (precocious males) within 2 or 3 days of their return in 1983 and 1985, respectively, to the Anadromous Inc. facility on Coos Bay. Scales had also been taken earlier from a subsample of each release group shortly before their release as smolts. Fork length at time of ocean entrance was backcalculated for each returning jack using the relationship between scale radius and fork length at the time of release for that group and other groups released in the same month. (Tag groups were grouped by month of release to obtain adequate numbers for the prerelease scale radius-fish length relationships). Ocean entrance was detected on the scale as an abrupt change in circulus spacing (see Fisher and Pearcy, 1988). Since these fish were released and returned to a site only 8 km from the ocean, their period of growth in the ocean should be very similar to the time between their release and return. Growth rate of each fish while in the ocean was estimated by $(FL_2 - FL_1)/d$, where FL_2 is length on return to the hatchery, FL_1 is the backcalculated length at time of ocean entry, and d is the days between release and return. Scale growth rate was estimated as $(SR_{tot} - SR_1)/d$, where SR1 is the scale radius to the ocean entrance mark, and SR_{tot} is the total scale radius. Mean circulus spacing during the ocean growth period was calculated as the distance between the first and last ocean circulus divided by $n - 1$, where n = the number of circuli laid down during ocean growth.

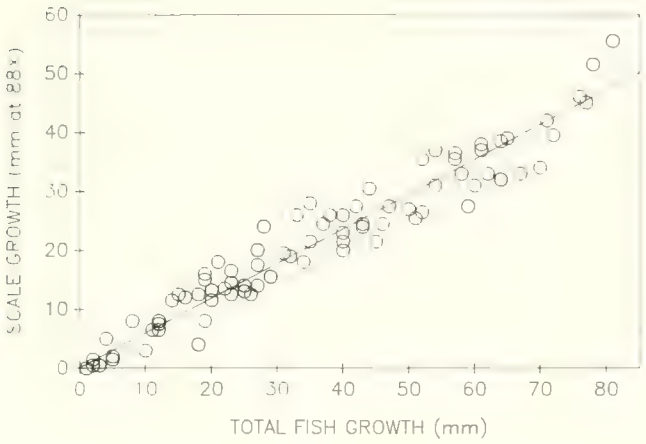

Figure 2
Scale growth vs. fish growth scattergram and GM regression line for individually marked age-0 smolts held in saltwater tanks.

Juvenile coho collected in the ocean

Growth rates in the ocean were estimated for CWT or spray-marked juvenile coho released (a) very near the ocean in Yaquina and Coos Bays and caught 60 or more days later in the ocean in August or September (15 fish), and (b) in the Columbia River (19 fish) and sampled during downstream migration near the ocean (at rkm 75, Dawley et al. 1985) and caught in the ocean 60 days or more after the median fish passed rkm 75, or released below rkm 75 and caught at least 60 days later in the ocean. For fish released in Yaquina or Coos Bays growth rate was estimated by $(FL_2 - FL_1)/d$ where FL_1 is the length at ocean entrance backcalculated from scales using a regression of FL on scale radius from a sample of fish taken at the time of release, FL_2 is length at capture in the ocean, and d is days between release and recapture. For Columbia River fish released in 1981, 1982, 1983, and 1984 length at ocean entrance was backcalculated using a regression of FL on scale radius derived from fish collected at rkm 75 in 1982 and 1983, combined. The number of days in the ocean was estimated from the date the median fish in each group passed rkm 75 and the mean downstream migration rates for each group. Estimated date of ocean entry for each group ranged from 3 to 11 days following passage of the median fish at rkm 75. For CWT Columbia River fish caught in 1984, when no sampling occurred at rkm 75, average downstream migration rates for tag groups from the same hatcheries in 1981–1983 were used in estimating ocean entrance date and days in the ocean (d). Scale growth rate for juvenile coho caught in the ocean was estimated the same way as for jacks.

Table 2
Rate of circulus formation (RCF, circuli per day) vs. fish growth rate (GR, mm/d): Correlation coefficients (r), probability that correlation = 0.0 (p), and geometric mean regression (GM) for age-0 fish held in saltwater tanks (A), CWT jacks (age 1.0) returning in 1983 (B) and 1985 (C), and CWT juvenile fish (both age 0.0 and 1.0) caught in the ocean (D).

Group	n	r	p	GM regression
A	80	0.89	<0.01	RCF = 0.18 · (GR) + 0.03
B	64	0.58	<0.01	RCF = 0.10 · (GR) + 0.03
C	99	0.57	<0.01	RCF = 0.10 · (GR) + 0.00
D	34	0.84	<0.01	RCF = 0.12 · (GR) + 0.02

Results

Fork length was positvely and significantly correlated with scale radius (SR) in all groups (Table 1, Fig. 1). The relationship (geometric mean regression, Ricker 1973) for each group of fish appeared linear. However, SR was smaller relative to FL for jacks returning in 1985 (diamonds in Figure 1) than for jacks returning in 1983 (squares) or for CWT juvenile coho salmon collected in the ocean (solid triangles). In addition, almost all FL–SR data points for returning yearling jacks and juveniles caught in the ocean were above the extrapolated regression line for the smaller subyearling fish held in saltwater tanks (Fig. 1). Thus, the relationships between FL and SR varied between age or size groups (small subyearling fish vs. larger yearling jacks and juveniles caught in the ocean) and between years (1983 vs. 1985 Anadromous Inc. jacks). The relationship between scale growth and fish growth appeared linear for the subyearling coho smolts held in saltwater tanks (Fig. 2).

Rate of circulus formation was positively and significantly (r = 0.57 – 0.89, $p<0.01$) correlated with fish growth rate for all groups (Table 2, Fig. 3). However the slope of the relationship was lower for ocean-caught juveniles and jacks returning in 1983 and 1985 (slopes of GM regression = 0.12, 0.10, 0.10, respectively) than for the subyearling fish held in saltwater tanks (slope = 0.17) At similar fish growth rates, rates of circulus formation were generally higher for the subyearling fish held in saltwater tanks than for juveniles caught in the ocean or for returning jacks (Fig. 3).

The spacing between circuli was positively and significantly correlated with fish growth rate for all groups but jacks returning in 1983 (Table 3). The correlation was strong (r = 0.80) for age 0.0 fish held in saltwater tanks, but much weaker for jacks returning in 1985 (r = 0.24). However, the relationship between circulus spacing and fish growth rate for subyearling

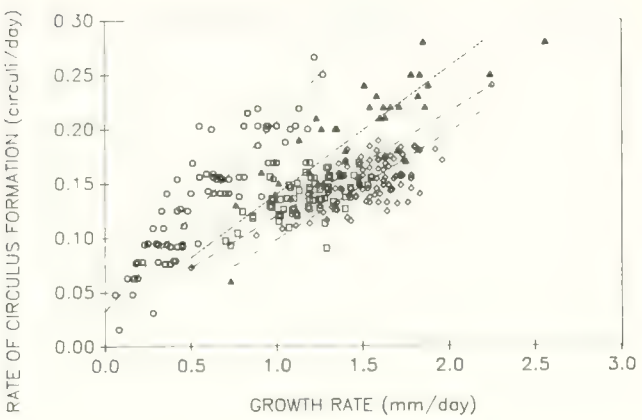

Figure 3

Rate of circulus formation vs. fish growth rate scattergrams and GM regression lines for age-0 smolts held in saltwater tanks (○, —), for CWT jacks returning to Coos Bay in 1983 (□, – –) and 1985 (◇, – –), and for CWT juvenile fish caught in the ocean (▲, – · · –).

Table 3

Circulus spacing (CSP, mm at 88×) vs. fish growth rate (GR, mm/d): Correlation coefficients (r), probability that correlation coefficient = 0.0 (p) and geometric mean regression (GM) for age-0 fish held in saltwater tanks (A), CWT jacks (age 1.0) returning in 1983 (B) and 1985 (C), and CWT juvenile fish (both ages 0.0 and 1.0) caught in the ocean (D).

Group	n	r	p	GM regression
A*	80	0.80	<0.01	CSP = 1.80 (GR) + 1.31
B	64	0.08	N.S.	
C	99	0.24	<0.05	CSP = 2.06 (GR) + 0.71
D	34	0.52	<0.01	CSP = 1.21 (GR) + 2.24

* For this group of fish the correlation coefficient for a third-order relationship, CSP = 0.91 + 5.35(GR) − 6.44(GR)^2 + 3.04(GR)^3, r = 0.83, was higher than for the linear relationship.

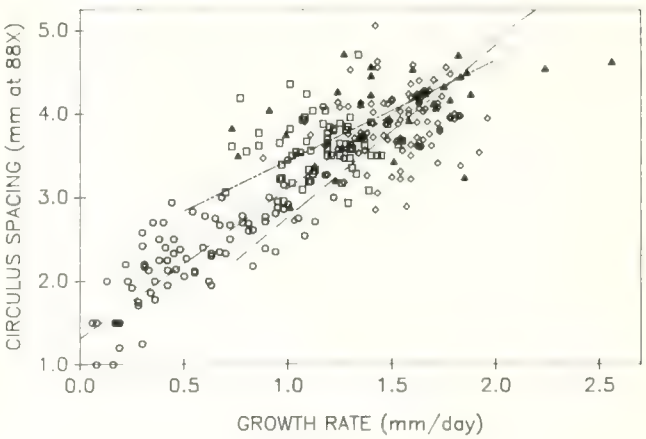

Figure 4

Circulus spacing vs. growth rate scattergrams and GM regression lines for age-0 smolts held in saltwater tanks (○, —), for CWT jacks returning to Coos Bay in 1983 (□, regression n.s.) and 1985 (◇, – –) and for CWT fish caught in the ocean (▲, – · · –).

fish held in saltwater tanks appeared to be nonlinear (see footnote, Table 3). In general, circulus spacing vs. growth rate values in the three groups that had reared in the ocean were fairly close to the extrapolated linear regression line for the smaller fish held in saltwater tanks, although the variability about this regression line was very large (Fig. 4). Mean growth rates of jacks returning in 1985 and juveniles caught in the ocean (1.49 mm/d and 1.53 mm/d, respectively) were significantly greater (t-tests, $p<0.01$) than the mean growth rate of jacks returning in 1983 (1.17 mm/d). Mean circulus spacings of the two faster growing groups (3.86 and 4.04 mm at 88× for jacks returning in 1985 and for juveniles caught in the ocean, respectively) were also both greater ($p<0.01$) than mean circulus spacing of the slower-growing jacks returning in 1983 (3.61).

In each group of fish some of the large variability in the relationship between circulus spacing or circulus deposition rate and fish growth rate was caused by variability in the relationship between fish length and scale radius. To remove this component of variation, we compared circulus spacing and circulus deposition rates with scale growth rates (Tables 4 and 5, respectively). Correlation coefficients for the relationships of circulus spacing and deposition rate with scale growth rate were considerably higher than for the corresponding relationships with fish growth rate, especially for jacks returning to Coos Bay in 1983 and 1985. (Compare Tables 2 with 4, and 3 with 5.) Circulus spacing was positively and significantly correlated with scale growth rate in all groups, whereas the relationship between circulus spacing and fish growth rate was significant for all groups but jacks returning in 1983. Thus, the correlations of circulus spacing or rate of circulus formation with scale growth rate were stronger than the correlations with the underlying fish growth rate.

Discussion

A positive correlation between rate of circulus formation and fish growth rate appears to be a common feature among fishes. We found in young coho salmon that rate of circulus deposition was positively and

Table 4

Rate of circulus formation (RCF, circuli/d) vs. scale growth rate (SGR, mm/d at 88×): Correlation coefficients (r), probability that correlation coefficient = 0.0 (p) and geometric mean regression (GM) for age-0 fish held in saltwater tanks (A),CWT jacks (age 1.0) returning in 1983 (B) and 1985 (C), and CWT juvenile fish (both age 0.0 and 1.0) caught in the ocean (D).

Group	n	r	p	GM regression
A	80	0.94	<0.01	RCF = 0.30(SGR) + 0.03
B	64	0.84	<0.01	RCF = 0.22(SGR) + 0.03
C	99	0.83	<0.01	RCF = 0.20(SGR) + 0.03
D	34	0.90	<0.01	RCF = 0.22(SGR) + 0.02

Table 5

Circulus spacing (CSP, mm at 88×) vs. scale growth rate (SGR, mm/d at 88×): Correlation coefficients (r), probability of correlation coefficient = 0.0 (p) and geometric mean regression (GM) for age-0 fish held in saltwater tanks (A), CWT jacks (age 1.0) returning in 1983 (B) and 1985 (C), and CWT juvenile fish (both age 0.0 and 1.0) caught in the ocean (D).

Group	n	r	p	GM regression
A*	80	0.82	<0.01	CSP = 3.07(SGR) + 1.29
B	64	0.62	<0.01	CSP = 4.22(SGR) + 1.39
C	99	0.59	<0.01	CSP = 4.14(SGR) + 1.56
D	34	0.56	<0.01	CSP = 2.26(SGR) + 2.22

* For this group of fish the correlation coefficient for a third order relationship, CSP = 1.02 + 6.92(SGR) − 10.37 $(SGR)^2$ + 6.77$(SGR)^3$, r = 0.84, was higher than for the linear relationship.

significantly correlated with scale and fish growth rates (Tables 2, 5; Fig. 3). Thus, the faster the fish or scales grew, the more circuli were formed per unit time. Positive correlations between rate of circulus formation and growth rate also have been found for walleye (Glenn and Mathias 1985) and cichlids (Sire 1986). In juvenile walleye, rate of circulus formation ranged from 1.5 circuli/d at high growth rates to 1 circulus every 2–3 weeks at low growth rates. Data presented by Bilton and Robins (1971a) indicated that juvenile sockeye salmon receiving more food, and presumably growing faster, produced more circuli during a given period than those fish that were fed less. Bilton and Robins (1971b) also found that sockeye salmon formed no circuli during periods of starvation. In chum salmon from Olsen Creek, Alaska, the number of circuli and radius to the middle of the first ocean annulus were positively correlated (Helle 1980). Therefore, if time to the middle of the first ocean annulus was constant (which may or may not be true), then fast-growing fish (larger radius) produced more circuli per unit time than slow-growing fish.

Positive correlations between circulus spacing and growth rate also have been reported in other species of fish. Bhatia (1932) found that scales from juvenile rainbow trout fed abundantly and growing rapidly, and scales from those fed sparsely and growing slowly had zones of widely spaced and narrowly spaced circuli, respectively, near the scale margin. Bhatia also was able to produce zones of widely and narrowly spaced circuli by alternately changing feeding level. Doyle et al. (1987) and Matricia et al. (1989) found positive correlations between circulus spacing and fish growth rate in tilapia. Sire (1986) found more widely spaced circuli among faster growing than slower growing cichlids. In juvenile walleye, mean spacing of circuli formed during the period of most rapid growth was found to be greater than mean spacing of circuli formed during periods of slower growth (Glenn and Mathias 1985). Bilton and Robins (1971a) found a significant positive correlation between feeding level and spacing of circuli in sockeye salmon.

Rate of circulus formation and spacing of circuli are probably related to a number of other factors beside growth rate. We found that rate of circulus formation for juvenile coho salmon caught in the ocean and especially for returning jacks were all well below the rates predicted by the regression for the much smaller fish held in saltwater tanks but growing at similar rates (Fig. 3). This suggests that the rate of circulus formation varies with age or size of fish or with environmental conditions, as well as with growth rate. Doyle et al. (1987) found that circuli of tilapia were laid down less frequently as fish grew larger. They also found that the relationship between growth rate and circulus spacing was stronger when a correction was made for the size of fish. Bilton (1975) suggested that rate of circulus deposition was probably a function of a combination of factors such as temperature, food, light, and maternal and inherent characteristics.

Several studies have addressed the possible effects of water temperature on circulus spacing. Generally they suggest that the effect of temperature, by itself, on circulus spacing is relatively small compared with the effect of feeding level or growth rate. By manipulating feeding level, Bhatia (1932) was able to produce zones of widely and narrowly spaced circuli in scales of rainbow trout growing in extremely different water temperatures (4°C and 17°C). Kimura and Sakagawa (1972), working with sardines, found that formation of annuli or checks (bands of narrowly spaced circuli) did not appear to be related to temperature. Barber and Walker (1988) found that in sockeye salmon annulus formation occurred before the coldest months of the

year and that during the coldest months widely spaced circuli were formed. Hogman (1968) cited work by Deason and Hile (1947) that indicated that annuli and checks formed in scales of kiyis living at depth in Lake Michigan, despite a very small annual variation in water temperature (2–3°C). Bhatia (1932) cited his earlier work showing that when rainbow trout were fed uniformly throughout the year no periodic zones were formed on their scales and all rings were of nearly the same width despite fluctuations in temperature. However, there is some evidence that in brown trout water temperature during egg and alevin stages prior to scale formation affected subsequent rate of circulus formation (Skurdal and Anderson 1985).

Inherent differences between groups of fish may mask the relationship between circulus spacing and growth rate. For example, for coho jacks returning to the Anadromous Inc. facility in Coos Bay in 1985, scales were generally smaller at a given fish length (Fig. 1), and rate of circulus formation was lower at a given growth rate (Fig. 2), than was the case for CWT juveniles caught in the ocean. This resulted in significantly different mean spacing of circuli in these two groups (3.86 vs. 4.04, t-test, $p<0.05$) despite very similar mean growth rates (1.53 and 1.49 mm/d, t-test, n.s.). Because of differences in the relationships between circulus spacing and growth rate among different groups of juvenile coho salmon, inferences about relative growth rates based on scale circulus spacing are probably only valid when made between groups that are similar in age, size, and morphometric characteristics (i.e., very similar SR–FL relationships).

Data from the group of subyearling fish held in saltwater tanks suggest that the relationship between circulus spacing and growth rate may be complicated. A third-order relationship (see footnote, Table 3) gave a better fit to the data than did a simple linear relationship. In this group of fish there was little change in circulus spacing between growth rates of 0.4 and 0.9 mm/d. More rapid changes in circulus spacing with growth rate occurred both above and below this range (circles, Fig. 4). This result suggests that for coho salmon there may be ranges of growth rates within which circulus spacing is a poor indicator of relative growth rate.

We compared mean circulus spacing in the ocean growth zone of scales for unmarked yearling (age 1.0) juvenile coho caught in the ocean in late summer of 1981, 1982, 1983, and 1984 (Fisher and Pearcy 1988). These fish had very similar SR–FL relationships in all years and were of similar size at time of entry into the ocean (based on backcalculated size at ocean entry). We also estimated growth rates of these unmarked juvenile yearling coho salmon between early and late summer (between June and August or September) from changes in mean lengths with time (see Fisher and Pearcy 1988, their Table 3). Rank order of mean spacing between circuli and growth rates estimated from shifts in mean FL with time are compared in Table 6. Although the rank orders do not agree in detail, they both suggest higher fish growth rates during the summers of 1981 and 1982 than in 1983 and 1984.

Table 6

Rank order of mean scale circulus spacing for unmarked juvenile coho collected in the ocean during the late summer, 1981–84, and growth rates of unmarked juvenile coho estimated from changes in mean length between early and late summer (see Fisher and Pearcy 1988, their Tables 3 and 4).

Year	Mean spacing (mm at 88 s)	Rank	Est. growth rate (mm/d)	Rank
1981	4.16	1	1.56	2
1982	4.15	2	1.76	1
1983	3.91	4	1.37	3
1984	3.95	3	1.33	4

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Abstract.—Optimal harvesting policies were developed for a model of the Washington-Oregon-California trawl fisheries for bocaccio *Sebastes paucispinus*, chilipepper *S. goodei*, widow rockfish *S. entomelas*, splitnose rockfish *S. diploproa*, and shortbelly rockfish *S. jordani*. In the simulated management system, the annual quota for each species was based on an intended fishing mortality rate (F) and an estimate of stock biomass. Traditional constant F policies were compared with variable F policies in which F was a linear function of either stock biomass (single-species) or the combined biomass of all other species (multispecies). Variable F policies were ineffective for increasing total harvest of all species combined, when compared with constant F policies. However, both single-species and multispecies variable F policies were found to reduce the variance for total harvest substantially with no significant loss in yield. The reduction in variance was roughly equal to the reduction that would be achieved by lowering the coefficient of variation (CV) for biomass estimates from 50% to 25% or from 25% to 0%. The reduction in variance generally was greater for the multispecies than for the single-species variable F policy. Compared with the case where CV = 0%, average total yield was reduced slightly for both constant F and variable F policies when CVs for biomass estimates were greater than 0%.

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Multispecies Harvesting Policies for Washington-Oregon-California Rockfish Trawl Fisheries

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In the Washington-Oregon-California (WOC) trawl fisheries for rockfish (*Sebastes* spp.), the landings are comprised of many species, including bocaccio *S. paucispinus*, chilipepper *S. goodei*, Pacific ocean perch *S. alutus*, canary rockfish *S. pinninger*, widow rockfish *S. entomelas*, and yellowtail rockfish *S. flavidus* (PFMC 1982). There is little evidence of substantial biological interaction among the adults of these species. Technological interactions (Pope 1979) are significant in the shelf rockfish fishery (Pikitch 1987), which accounts for most of the landings of bocaccio, chilipepper, and canary and yellowtail rockfish. Fishermen have some control over the species composition of the catch in this fishery by varying the areas or depths fished. The other significant rockfish fishery is the midwater trawl fishery for widow rockfish. Catches of other rockfish species are negligible in that fishery.

Most currently marketed *Sebastes* species have similar or equal value to fishermen; consequently, fishermen are more concerned about the aggregate yield than about the species composition of the catch. Thus, it seems reasonable to ask whether efforts to vary the annual proportions harvested for these species would result in benefits to the resource or to the fishing industry. For example, reducing the variability of annual quotas has been an important concern for the west coast fishing industry. The objective of this study was to evaluate multispecies harvesting policies for the WOC trawl fisheries for rockfish to determine whether total yield (all species combined) can be increased or the variance for total yield can be reduced. Specifically, I compared the performance of policies obtained using (1) risk-neutral and risk-averse objective functions, (2) constant and variable fishing mortality rates (F), and (3) abundance estimates for a single species or multiple species.

Except for widow rockfish, relatively little is known about the population dynamics of these stocks. For that reason, this study should be viewed as an exploratory analysis of alternative harvesting policies, and not as a basis for regulatory changes by the Pacific Fishery Management Council. It may be worthwhile to develop similar harvesting policies for Council review once we have adequate life-history information about the commercially important groundfish stocks. The harvesting policies examined in this study should be useful in other cases where fishermen derive income from several species and have some control over the species composition of the catch.

Methods

This section provides an overview of the model structure, harvesting policies, and life-history data. A detailed description of methods is provided elsewhere (Hightower 1990).

I developed optimal harvesting policies for two-, three-, and five-

species models in order to evaluate changes in policy performance as additional species were included. The selected species (bocaccio, chilipepper, widow rockfish, splitnose rockfish *S. diploproa*, and shortbelly rockfish *S. jordani*) all occur off California, support or could support significant commercial fisheries, and have a wide range of life-history types. I used bocaccio and chilipepper for the two-species model because they were estimated to have similar biomass levels. I included widow rockfish for the three-species model because it was estimated to have about twice the maximum sustainable yield level of biomass of bocaccio and chilipepper. For the five-species model, shortbelly and splitnose rockfish were added as examples of relatively short- and long-lived rockfish species, respectively. Shortbelly rockfish biomass also is substantially higher than that of the other four species.

Model structure

I used Schnute's (1985) generalization (eq. 2.7) of Deriso's (1980) delay-difference model to represent the dynamics of each stock:

$$B_t = (1+\rho)S_{t-1}B_{t-1} - \rho S_{t-1}S_{t-2}B_{t-2} + R_t - \rho(v/V)S_{t-1}R_{t-1} \quad (1)$$

where B_t was the fishable population biomass at the beginning of year t; S_t was the survival rate in year t; ρ, v, and V were parameters for the growth curve; and R_t was the recruitment biomass at the beginning of year t. Growth parameters ρ, v, and V were estimated by fitting the following curve relating mean weight at age a (w_a) to age:

$$w_a = v + (V - v)(1 - \rho^{1+a-k})/(1-\rho) \quad (2)$$

where V and v were parameters representing mean weight at the age of recruitment (age k) and at age k – 1, respectively, and ρ was a parameter describing the growth rate (Schnute 1985, eq. 1.14). Following Kimura et al. (1984), I assumed that B_0 (needed to calculate B_2) equaled the starting biomass level B_1.

Recruitment was calculated from a Beverton-Holt stock-recruitment curve (Kimura 1988):

$$R_{t+1} = R_\infty(B_t/B_\infty)/(1 - A(1 - B_t/B_\infty))\exp(z_t) \quad (3)$$

where R_∞ was the virgin recruitment level associated with virgin stock biomass B_∞, A was the level of density-dependence assumed in the stock-recruitment relationship, and $\exp(z_t)$ was the lognormal error term used to introduce random variability in recruitment. Estimates of A were not available for any of the stocks used in this study. To introduce a degree of density-dependence into the model, I assumed arbitrarily that recruitment decreased by 10% when spawning stock decreased by 50%. That assumption has been used in earlier stock-assessment studies (Lenarz 1984, Henry 1986, Methot and Hightower 1988, Tagart 1988) to obtain harvest recommendations assumed to be conservative when information on the stock-recruitment relationship was unavailable. The normal random variate z_t was assumed to have mean 0 and variance σ^2. I assumed that $R_1 . . R_k$ were produced by a stock equal in size to B_1 because the actual B values producing those year-classes were not known.

Harvesting policies

In the harvesting policies used in this study, the annual fishing mortality rate for species j in year t ($F_j[t]$) was either a constant

$$F_j[t] = b_{j,0} \quad \text{(constant F)}, \quad (4)$$

a function of stock biomass

$$F_j[t] = b_{j,0} + b_{j,1} B_j[t] / B_{\infty,j} \quad \text{(variable F)}, \quad (5)$$

or a function of the combined biomass of all other stocks

$$F_j[t] = b_{j,0} + b_{j,1} \sum_{i \neq j} B_i[t] / \sum_{i \neq j} B_{\infty,i}, \quad \text{(multispp. var. F)} \quad (6)$$

Policies (5) and (6) were similar in form to a linear model Hilborn (1985) used to calculate catch as a function of stock biomass. Biomass estimates were scaled by virgin biomass so that the policy parameters were relatively independent of absolute biomass levels. Estimates of the policy parameters ($b_{j,0}$, $b_{j,1}$; j = 1, . . , s species in model) were obtained using stochastic approximation (Ruppert et al. 1984).

Objective functions

As in earlier optimization studies (Ruppert et al. 1984, Hilborn 1985), I obtained policies for maximizing total catch

$$\max \sum_t C[t], \text{ where } C[t] = \sum_j C_j[t] \quad \text{(maxh objective function)}$$

and the natural logarithm of total catch

$$\max \sum_t \log(C[t]) \qquad \text{(logh objective function).}$$

For most of the WOC trawl fisheries, the goal of the Pacific Fishery Management Council is to maximize long-term average yield by maintaining F at a specified level. Thus the maxh objective function corresponds to the current approach to management. Relative to maxh policies, logh policies tend to provide less variable catches so they may be more appropriate in fisheries where price is sensitive to volume, the fishery provides a substantial fraction of a fisherman's annual income, or stability of volume is critical for marketing reasons (Deriso 1985). Mendelssohn (1982) and Ruppert et al. (1985) used maxh and logh policies to represent extremes along a risk continuum, in that maxh policies are risk-neutral (marginal utility does not change with increasing catch) and logh policies are risk-averse (marginal utility decreases with increasing catch).

I also evaluated a third more conservative objective function for maximizing an exponential function of total catch:

$$\max \sum_t (1 - \exp(-C[t]/\delta)) \quad \text{(negx objective function)}$$

where δ was a scaling factor (Raiffa 1968). At small values of δ (relative to C[t]), the marginal utility of additional units of catch decreases rapidly. If δ is large, utility increases linearly with increasing catch. In order to obtain highly risk-averse policies, I used $\delta = 5$ for C[t] values of about 5 (2-species case) to 30 (5-species case). Using this δ value, negx policies were even more conservative than logh policies (Fig. 1). Of course, other objective functions (and harvesting policies) could be chosen that would provide greater reductions in the variance of catch. For example, Murawski and Idoine (1989) compared a series of constant-catch harvesting policies for Georges Bank haddock *Melanogrammus aeglefinus*. For a sufficiently low target catch (45% of the average catch under a constant $F = F_{0.1}$ policy), year-to-year variability in catch was zero. The logh and negx objective functions used in this study were intended to provide a compromise between maximizing catch and minimizing variability of catch.

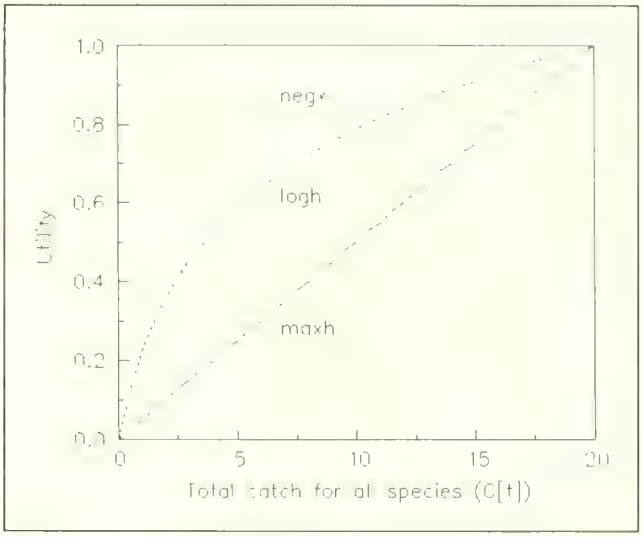

Figure 1

Alternative measures of the utility of the total rockfish catch in year t (C[t]), as determined by objective functions maxh:Utility(C[t]) = C[t], logh:Utility(C[t]) = $\log_e$(C[t]), and negx:Utility(C[t]) = $1 - \exp(-C[t]/5)$. Utilities for each objective function were scaled to a maximum value of 1.

Planning horizon

The optimization studies were done using a 100-year planning horizon in order to obtain steady-state harvesting policies. In the two- and three-species cases, the bocaccio, chilipepper, and widow rockfish stocks declined to varying degrees at the start of the planning horizon but reached steady-state levels by about year 50 (Fig. 2). In the five-species case, sharp initial declines were noted for the unexploited splitnose and shortbelly rockfish stocks. Because of its long life-span and slow growth-rate, the splitnose rockfish stock continued to decline throughout the planning horizon. Based on a series of optimization runs, I found that the constant F for splitnose rockfish that maximized mean harvest decreased as the horizon length increased for policies up to 200 years in length. Planning horizons greater than 100 years were impractical, however, due to computing costs. Therefore, in order to obtain results that were not dependent on the length of the planning horizon, I obtained policies for the five-species model using a 75-year transient phase within a 100-year horizon (Law and Kelton 1982). Using this approach, the objective function was based only on harvests in years 75–100. Steady-state biomass levels were reached within 100 years for all species except possibly splitnose rockfish; thus, declines in stock size at the start of the planning horizon were due only to high initial biomass levels (Fig. 3).

Errors in biomass estimates

Most of the harvesting policies evaluated in this study required biomass estimates for one or more species in order to calculate the policy Fs used to determine the annual quotas. To evaluate the practicality of these policies, I introduced a random error term so that the harvesting policy and resultant catch quota in year t were based on simulated estimates $B'_1[t] \ldots B'_s[t]$ of

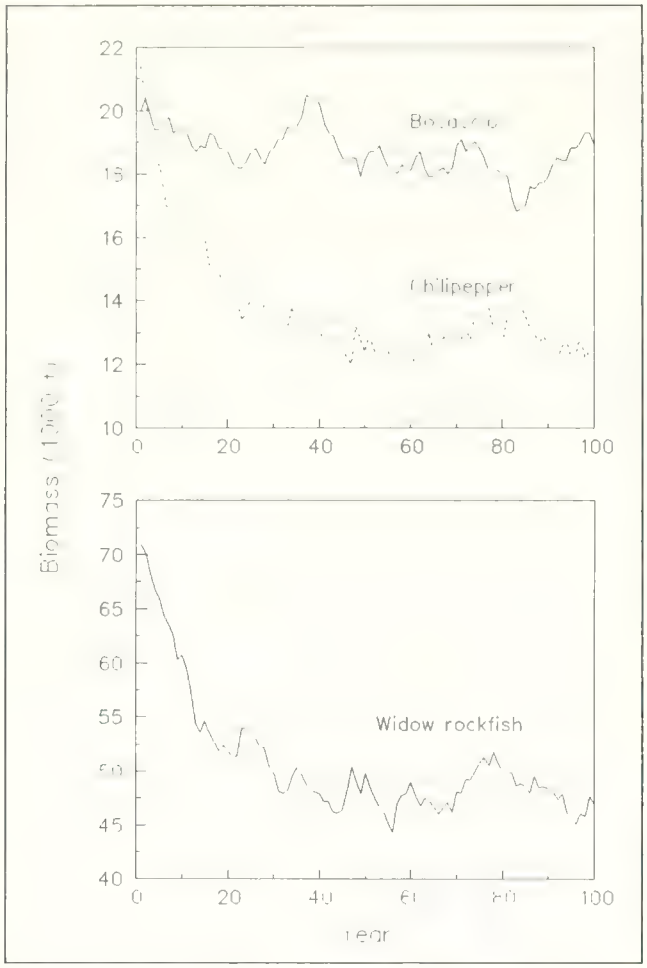

Figure 2

Mean rockfish biomass from 100 replicate 100-year simulation runs for the three-species model, using the constant fishing mortality rates that maximized harvest and assuming that the coefficient of variation for biomass estimates was 0. Results for the two-species model with only bocaccio and chilipepper were similar and are not shown here.

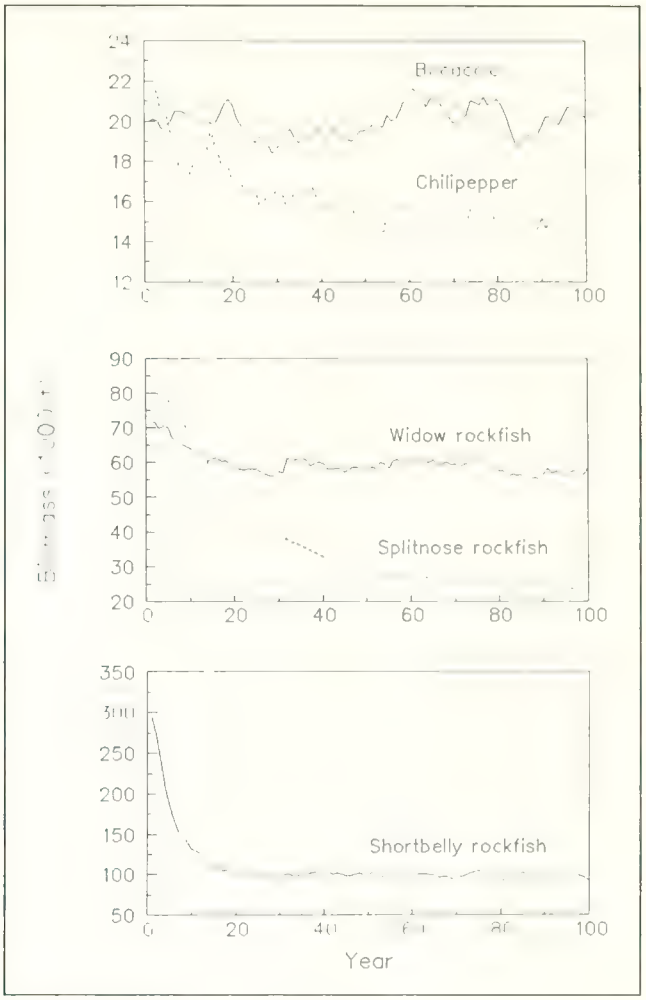

Figure 3

Mean rockfish biomass from 100 replicate 100-year simulation runs for the five-species model, using the constant fishing mortality rates that maximized harvest and assuming that the coefficient of variation for biomass estimates was 0.

the actual biomass levels $B_1[t]..B_s[t]$. Following an assumption made by Pope and Gray (1983) regarding data used in stock assessments, I assumed that errors in biomass estimates were lognormally distributed and independent over time. The coefficient of variation (CV) for biomass estimates was either 0, 25, or 50%, based on a review of the stock-assessment literature (Rivard 1981, Pope 1983, Pope and Gray 1983, Sen 1984, Weinberg et al. 1984, Methot 1986).

Because the WOC trawl fisheries for rockfish are regulated through catch quotas, F′ (the policy F based on estimates $B'_1[t]..B'_s[t]$) was used to calculate the annual quota $C_j[t]$ as $B'_j[t]F'_j[t](1-\exp(-M_j-F'_j[t])/Z'_j[t]$. $B_{\infty,j}$ (the virgin biomass level used in the variable F policies) and M_j were assumed to be known without error. The actual F required to obtain $C_j[t]$ from $B_j[t]$ ($F_j[t]$) was either higher or lower than the intended F ($F'_j[t]$), depending on the direction and magnitude of errors in $B'_1[t]..B'_s[t]$.

Life-history information

The reliability of the parameter estimates (Table 1) varies, depending on the length and magnitude of the historical fishery for each species. A significant fishery for widow rockfish developed in 1979, with average 1980–85 landings of 17200 t (Hightower and Lenarz 1986). Fisheries for bocaccio and chilipepper have existed for decades; average 1980–85 landings were 3200 t for bocaccio and 1700 t for chilipepper (PFMC 1986). Preliminary stock assessments based on catch-at-age data have been completed for all three species. Land-

Table 1

Parameters used in delay-difference models for each rockfish species. Methods used to estimate the life-history parameters are described in detail by Hightower (1990).

	widow	bocaccio	chilipepper	splitnose	shortbelly
k	6	4	8	12	4
v (kg)	0.436	0.061	0.581	0.327	0.078
V (kg)	0.598	0.553	0.796	0.343	0.110
ρ	0.903	0.933	0.878	0.984	0.825
M	0.15	0.25	0.20	0.05	0.20
B_∞ (t)	180.0	60.0	47.7	80.0	295.0
B[1] (t)	71.0	20.0	21.4	80.0	295.0

Table 2

Fishing mortality rates of rockfish obtained for constant F policies maximizing harvest (maxh), log(harvest) (logh), or a negative exponential function of harvest (negx) for two-, three-, and five-species models.

		Fishing mortality rate				
Species	Objective function	bocaccio	chilipepper	widow	splitnose	shortbelly
Two	maxh	0.200	0.269	–		–
	logh	0.195	0.255	–	–	–
	negx	0.194	0.250	–		–
Three	maxh	0.201	0.264	0.181		–
	logh	0.196	0.254	0.174	–	
	negx	0.191	0.242	0.163	–	
Five	maxh	0.182	0.222	0.153	0.056	0.229
	logh	0.181	0.218	0.152	0.055	0.224
	negx	0.187	0.211	0.146	0.055	0.204

ings of splitnose and shortbelly rockfish have been negligible to date; consequently, parameter estimates for those species should be viewed as highly preliminary.

Results and discussion

Objective functions

Results were similar for constant F policies using different objective functions. Optimal constant Fs generally were comparable with M, although the F for chilipepper (M = 0.20) was higher than that for bocaccio (M = 0.25) (Table 2). That apparently was due to the higher age at first recruitment for chilipepper. (For bocaccio and chilipepper, the slight differences in constant Fs in the two- and three-species cases were due to random error.) Optimal Fs were lower for the five-species case than for the two- and three-species cases because harvests in years 1–74 were excluded from the five-species objective function. Policies obtained assuming a transient period may be unacceptable on socio-economic grounds but can probably be viewed as a practical lower bound for F.

For each of the models, the differences in F, total yield, and variance for total yield showed a consistent trend: highest for maxh policies, intermediate for logh policies, and lowest for negx policies (Tables 2–5). Relative to the variance for maxh policies, logh constant F policies resulted in about a 2% reduction in total variance, whereas variances for the negx policies were 3 (2-species case) to 10% (5-species case) lower. These results illustrate that moderately lower variances can be achieved by using slightly lower Fs and accepting slightly lower total yields.

Constant vs. variable F policies

The variable F policies (5)–(6) for maximizing harvest did not increase total yield significantly compared to the constant F policies (Tables 3–5). Results from earlier studies suggest that the degree of increase due to a variable F policy may depend on the assumed life-history characteristics. For example, a 17% increase

Table 3

Comparison of average rockfish catches and year-100 variances for constant F, single-species variable F, and multispecies harvesting policies. CVs for biomass estimates were assumed to be 0%.

			Mean yield						Var[100]					
Species	Harvesting policy	Objective function	bocaccio	chili-pepper	widow	split-nose	short-belly	total	bocaccio	chili-pepper	widow	split-nose	short-belly	total
Two	const F	maxh	3.02	2.96	–	–	–	5.98	0.97	1.46	–	–	–	2.87
		logh	3.02	2.96	–	–	–	5.98	0.96	1.42	–	–	–	2.81
		negx	3.02	2.95	–	–	–	5.97	0.95	1.40	–	–	–	2.78
	variable F	maxh	3.05	3.02	–	–	–	6.05	1.49	3.81	–	–	–	6.00
		logh	3.03	2.96	–	–	–	5.96	0.91	1.17	–	–	–	2.44
		negx	3.02	2.95	–	–	–	5.95	0.84	1.09	–	–	–	2.27
	multispp.	maxh	3.02	2.96	–	–	–	5.98	0.95	1.48	–	–	–	2.83
		logh	3.00	2.95	–	–	–	5.95	0.92	1.36	–	–	–	1.94
		negx	2.99	2.94	–	–	–	5.93	0.95	1.32	–	–	–	1.70
Three	const F	maxh	3.02	2.95	7.78	–	–	13.75	1.01	1.28	4.92	–	–	7.40
		logh	3.04	2.94	7.77	–	–	13.75	1.01	1.26	4.85	–	–	7.29
		negx	3.03	2.93	7.75	–	–	13.71	1.00	1.23	4.72	–	–	7.12
	variable F	maxh	3.06	3.01	7.92	–	–	13.93	1.47	3.08	14.12	–	–	18.55
		logh	3.05	2.97	7.82	–	–	13.78	1.18	1.34	4.86	–	–	7.59
		negx	3.03	2.93	7.70	–	–	13.61	0.93	1.04	3.72	–	–	5.75
	multispp.	maxh	3.03	2.94	7.77	–	–	13.74	1.01	1.28	4.96	–	–	7.74
		logh	3.02	2.94	7.75	–	–	13.70	1.02	1.26	4.68	–	–	5.60
		negx	2.98	2.91	7.70	–	–	13.60	1.06	1.20	4.36	–	–	4.08
Five	const F	maxh	3.04	2.85	7.82	1.97	19.92	35.59	1.13	0.74	5.90	0.08	69.56	78.05
		logh	3.05	2.86	7.84	1.94	19.93	35.48	1.13	0.73	5.86	0.08	67.97	76.42
		negx	3.05	2.85	7.82	1.94	19.58	35.09	1.14	0.72	5.73	0.08	61.90	70.19
	variable F	maxh	3.06	2.90	7.95	2.30	20.84	36.91	1.53	1.22	16.96	0.21	431.37	460.41
		logh	3.06	2.89	7.91	2.43	20.02	36.17	1.40	0.84	7.56	0.25	70.84	82.13
		negx	3.03	2.85	7.70	1.49	18.58	33.53	0.99	0.70	3.70	0.20	26.41	32.10
	multispp.	maxh	3.03	2.87	7.85	1.99	20.07	35.67	1.18	0.74	5.90	0.08	70.92	78.16
		logh	2.89	2.58	7.52	1.37	19.61	33.83	1.28	0.93	6.01	0.63	68.64	44.60
		negx	2.46	2.64	7.72	1.41	19.37	33.46	1.64	0.69	5.52	0.20	59.66	43.70

in yield was reported for Atlantic menhaden *Brevoortia tyrannus* (Ruppert et al. 1985), compared with only 1–2% for Pacific whiting *Merluccius productus* (Swartzman et al. 1983) and widow rockfish (Hightower and Lenarz 1989). Because, in this study, there was no apparent advantage in using variable F policies to maximize harvest, the remaining results and discussion focus on a comparison of the traditional constant F policy for maximizing harvest versus variable F policies (5) and (6) for the logh and negx objective functions.

Compared with a constant F policy, variable F policies (5) and (6) provided a substantial reduction in the variance of total yield with only a negligible loss in yield. (The reductions in variance would be slightly less if constant F and variable F policies for the same objective function were compared.) The reduction in variance did not appear to be particularly sensitive to the number of species included, their life-history characteristics, or the degree of correlation among species for recruitment perturbations (Hightower 1990). However, the level of density-dependence in the stock-recruitment relationship may affect the relative performance of different harvesting policies. In limited additional runs, I found that the difference between constant F and variable F policies generally decreased as the degree of density-dependence increased (i.e., as stock-recruitment parameter A decreased). When recruitment declined markedly with reductions in spawning stock, both types of harvesting policies were necessarily quite conservative.

The advantage of the variable F policies can be illustrated by examining a Pareto Frontier (Walters 1975), which shows the relationship between mean catch and its variance. I developed frontiers for the two-, three-, and five-species cases by simulating the fishery at 20, 40, 60, 80, and 100% of the constant F levels that maximized harvest (Fig. 4). When results for the variable F policies were compared to the constant F frontiers, it was clear that the reduction in variance was much greater than could be accounted for by the lower yield

Table 4

Comparison of average rockfish catches and year-100 variances for constant F, single-species variable F, and multispecies harvesting policies. CVs for biomass estimates were assumed to be 25%.

			Mean yield						Var[100]					
Species	Harvesting policy	Objective function	bocaccio	chili-pepper	widow	split-nose	short-belly	total	bocaccio	chili-pepper	widow	split-nose	short-belly	total
Two	const F	maxh	3.01	2.95	—	—	—	5.97	1.66	2.05	—	—	—	4.10
		logh	3.01	2.95	—	—	—	5.96	1.65	2.01	—	—	—	4.04
		negx	3.01	2.95	—	—	—	5.96	1.64	2.00	—	—	—	4.02
	variable F	maxh	3.04	3.00	—	—	—	6.02	3.33	5.57	—	—	—	9.60
		logh	3.01	2.95	—	—	—	5.93	1.28	1.41	—	—	—	3.00
		negx	3.00	2.93	—	—	—	5.91	1.17	1.26	—	—	—	2.72
	multispp.	maxh	3.01	2.95	—	—	—	5.97	1.65	2.06	—	—	—	4.10
		logh	2.99	2.94	—	—	—	5.92	1.79	1.96	—	—	—	2.44
		negx	2.98	2.93	—	—	—	5.90	1.86	1.95	—	—	—	2.25
Three	const F	maxh	3.03	2.94	7.76	—	—	13.72	1.61	2.05	8.58	—	—	11.58
		logh	3.02	2.94	7.75	—	—	13.72	1.61	2.03	8.51	—	—	11.50
		negx	3.02	2.93	7.73	—	—	13.68	1.60	2.00	8.39	—	—	11.34
	variable F	maxh	3.03	2.99	7.84	—	—	13.80	6.48	4.66	11.25	—	—	22.37
		logh	3.04	2.95	7.74	—	—	13.67	1.58	1.78	6.09	—	—	9.01
		negx	3.01	2.92	7.65	—	—	13.53	1.16	1.48	5.16	—	—	7.47
	multispp.	maxh	3.03	2.94	7.76	—	—	13.72	1.61	2.04	8.56	—	—	12.17
		logh	3.01	2.93	7.73	—	—	13.67	1.83	2.15	8.73	—	—	7.97
		negx	2.93	2.88	7.72	—	—	13.53	2.33	2.36	8.39	—	—	6.01
Five	const F	maxh	3.04	2.86	7.84	1.97	20.00	35.56	1.64	1.26	7.06	0.19	108.60	120.11
		logh	3.04	2.86	7.82	1.97	19.92	35.46	1.63	1.25	7.03	0.19	105.84	117.31
		negx	3.03	2.83	7.80	1.91	19.54	34.96	1.62	1.22	6.95	0.18	96.32	107.63
	variable F	maxh	3.05	2.89	7.90	2.33	20.70	36.74	2.88	3.95	14.34	2.75	958.44	987.02
		logh	3.04	2.87	7.84	2.25	19.55	35.43	1.80	1.54	6.71	0.34	66.07	78.42
		negx	2.99	2.82	7.66	2.22	18.10	33.67	1.04	0.84	4.70	0.34	31.20	40.20
	multispp.	maxh	3.01	2.86	7.84	2.00	20.01	35.59	1.71	1.27	7.07	0.19	107.71	115.41
		logh	2.91	2.56	7.35	1.39	19.60	33.66	1.82	1.51	8.72	1.13	110.50	66.74
		negx	2.22	2.31	7.08	1.14	19.47	32.09	2.79	1.77	9.08	1.48	95.97	40.77

obtained. In some cases, the reduction was comparable to the reduction that would be achieved by lowering the CVs for biomass estimates from 50% to 25% or from 25% to 0%. The percent reduction typically increased as the CVs for biomass estimates increased, although the loss in mean yield also increased somewhat (Hightower 1990).

Single-species vs. multispecies policies

When single-species (5) and multispecies (6) policies were compared, the variance for total catch generally was lower for the multispecies policy, except for some cases for the five- species model or when biomass CVs were 50%. In those cases, the better performance of the single-species policy probably was due to the feedback mechanism it contained. For example, in the five-species models, the single-species policies for shortbelly and splitnose rockfish could adapt to the large changes in the size of those stocks. When the five-species model was rerun using five "stocks" having chilipepper life-history characteristics, the variance for total catch was lower for the multispecies policy.

For the single-species policy, the variance of total catch typically was reduced by stabilizing the catch of each individual species (Tables 3–5). For the multispecies policy, reductions in the variance for total catch were sometimes achieved by increasing the variance for some of the less abundant individual species (Tables 3–5). The reduction in variance obtained using policy (6) is consistent with Clark's (1984) prediction that a multispecies system could be managed to reduce the variance of total yield, relative to the variance of the individual yields.

For the multispecies policies, the optimal parameter estimates were relatively insensitive to the objective function and to the CV for biomass estimates (Hightower 1990). The slope parameter $b_{j,1}$ was less than zero for all cases; consequently, fishing pressure varied inversely with the abundance of the other species.

Table 5

Comparison of average rockfish catches and year-100 variances for constant F, single-species variable F, and multispecies harvesting policies. CVs for biomass estimates were assumed to be 50%.

			Mean yield						Var[100]					
Species	Harvesting policy	Objective function	bocaccio	chili-pepper	widow	split-nose	short-belly	total	bocaccio	chili-pepper	widow	split-nose	short-belly	total
Two	const F	maxh	3.00	2.94	–	–	–	5.93	3.40	3.63	–	–	–	7.39
		logh	3.00	2.93	–	–	–	5.93	3.38	3.59	–	–	–	7.33
		negx	2.99	2.93	–	–	–	5.92	3.38	3.58	–	–	–	7.31
	variable F	maxh	3.02	2.97	–	–	–	5.96	8.49	12.36	–	–	–	21.14
		logh	2.97	2.91	–	–	–	5.85	1.84	1.83	–	–	–	4.06
		negx	2.95	2.90	–	–	–	5.83	1.68	1.69	–	–	–	3.77
	multispp.	maxh	3.00	2.94	–	–	–	5.93	3.40	3.65	–	–	–	7.48
		logh	2.96	2.91	–	–	–	5.87	4.04	3.76	–	–	–	4.24
		negx	2.96	2.90	–	–	–	5.86	4.06	3.91	–	–	–	4.09
Three	const F	maxh	3.01	2.92	7.72	–	–	13.65	3.35	4.42	19.06	–	–	24.74
		logh	3.01	2.92	7.72	–	–	13.64	3.35	4.37	19.03	–	–	24.70
		negx	3.01	2.91	7.69	–	–	13.61	3.34	4.30	18.90	–	–	24.53
	variable F	maxh	3.02	2.94	7.78	–	–	13.70	11.44	6.07	33.98	–	–	48.11
		logh	3.00	2.92	7.66	–	–	13.53	2.17	2.64	10.35	–	–	14.49
		negx	2.97	2.88	7.58	–	–	13.37	1.66	2.02	9.47	–	–	12.76
	multispp	maxh	3.01	2.92	7.72	–	–	13.65	3.43	4.42	18.91	–	–	24.88
		logh	2.97	2.89	7.69	–	–	13.55	4.58	5.09	20.90	–	–	15.79
		negx	2.91	2.84	7.68	–	–	13.43	6.01	5.34	20.42	–	–	13.29
Five	const F	maxh	3.02	2.84	7.80	1.96	19.84	35.32	3.15	3.87	15.26	0.47	192.76	219.04
		logh	3.02	2.84	7.78	1.96	19.73	35.18	3.14	3.85	15.21	0.47	188.46	214.56
		negx	3.02	2.82	7.72	1.95	19.38	34.75	3.16	3.80	14.96	0.47	177.72	203.35
	variable F	maxh	3.03	2.86	7.81	2.18	20.43	36.18	5.26	10.09	120.32	4.15	1356.71	1540.97
		logh	3.02	2.82	7.78	1.43	18.64	33.56	2.90	1.52	11.61	0.54	64.10	84.87
		negx	2.96	2.78	7.51	1.52	17.32	31.96	1.53	1.26	7.28	0.42	43.02	55.69
	multispp.	maxh	3.00	2.84	7.79	1.97	19.91	35.38	3.34	3.88	15.26	0.47	191.10	209.32
		logh	2.92	2.64	7.44	1.57	19.58	34.01	3.58	3.45	18.95	1.68	208.31	135.32
		negx	2.08	2.28	7.05	1.37	19.20	31.84	7.13	4.10	20.26	2.46	173.92	81.64

Particularly in the three- and five-species cases, it appeared that the optimal multispecies strategy was to maintain stable catches for the species accounting for the majority of total yield, such as shortbelly or widow rockfish. Catches of less-abundant species (e.g., bocaccio or splitnose rockfish) varied depending on the abundance of the dominant species. For example, in the five-species case, the annual catch of splitnose rockfish was 0 in 24–30 of 100 years for the logh policies.

Errors in biomass estimates

Constant F policies were essentially identical when different CVs for biomass estimates were used. This indicates that the current management approach for Pacific Coast groundfish is robust to random, non-autocorrelated errors in estimating biomass. One obvious impact in the simulated fishery of introducing errors in estimating biomass was that the variance for total catch increased substantially (Tables 3–5, Fig. 4). This increased variability was due to differences between the intended (F) and actual (F′) fishing mortality rate. Such errors are nonlinearly related to estimated stock size and can be substantial (Rivard 1981). Rivard (1981) argued for higher precision in estimates of stock size in order to reduce the biological risk of applying $F' \gg F$ or the economic loss if $F' \ll F$. In this study, the variation in F due to errors in estimating biomass was much greater than that caused by using the variable F policies. For example, when CV = 0%, Fs for chilipepper in the five-species case ranged from 0.00 to 0.24 when using the multispecies logh model. When CV = 25%, the actual Fs ranged from 0.06 to 0.61 when the intended policy was a constant F of 0.22. Actual Fs ranged from 0.00 to 0.63 when CV = 25% and a multispecies logh policy was used, which suggests that multispecies policies do not introduce substantial additional risk, relative to the risk introduced by estimating biomass with error.

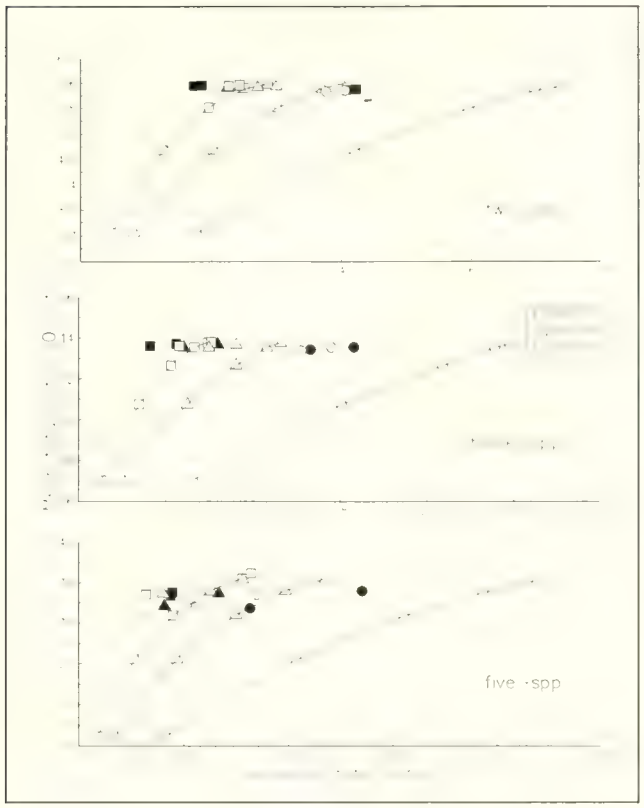

Figure 4

Relationship between mean total rockfish catch and the variance of total catch for the two- (bocaccio, chilipepper), three- (bocaccio, chilipepper, widow rockfish), and five-species (bocaccio, chilipepper, widow, splitnose, and shortbelly rockfish) models. Open symbols represent Pareto Frontiers derived by simulating the fishery at 20, 40, 60, 80, and 100% of the constant fishing mortality rate (F) that maximized harvest. Shaded and closed symbols represent the catch:variance relationship for the variable F and multispecies policies, respectively (equations 5–6). Simulation runs were made assuming a 0, 25, or 50% coefficient of variation for annual estimates of stock size.

Table 6

Average total rockfish catches and year-100 variances for constant F, variable F, multispecies, and three-parameter harvesting policies for the three-species model.

Biomass CVs	Policy	Objective function	Yield	Var[100]
0	(4)	maxh	13.75	7.40
	(5)	logh	13.78	7.59
	(6)	logh	13.70	5.60
	(7)	logh	13.77	6.39
	(5)	negx	13.61	5.75
	(6)	negx	13.60	4.08
	(7)	negx	13.60	4.09
25	(4)	maxh	13.72	11.58
	(5)	logh	13.67	9.01
	(6)	logh	13.67	7.97
	(7)	logh	13.63	6.99
	(5)	negx	13.53	7.47
	(6)	negx	13.53	6.01
	(7)	negx	13.51	5.40
50	(4)	maxh	13.70	24.74
	(5)	logh	13.53	14.49
	(6)	logh	13.55	15.79
	(7)	logh	13.50	11.39
	(5)	negx	13.37	12.76
	(6)	negx	13.43	13.29
	(7)	negx	13.33	8.21

Mean yield was only slightly lower at higher biomass CVs; the decrease was similar for constant F and variable F policies (Tables 3–5). Thus, in this model at least, there was no apparent disadvantage in using the more complex policies, even when biomass was estimated imprecisely. This was an interesting result because, although all policies used biomass estimates to calculate catch, the variable F policies also use the estimates to calculate Fs.

When biomass CVs were 50%, the variance for total catch was in all cases lower for the single-species (5) than for the multispecies policy (6). Apparently it was important to readjust continuously for the changes in stock size due to previous errors in estimating biomass. Based on limited additional runs using the three-species model, it appears that further gains in stability of total catch could be achieved by using a three-parameter harvesting policy (Table 6):

$$F_i[t] = b_{i,0} + b_{i,1} B_i[t] / B_{\infty,i} + b_{i,2} \sum_{j \neq i} B_i[t] / \sum_{j \neq i} B_{\infty,j}. \quad (7)$$

The primary disadvantage of this policy is the computational expense required to obtain the policy parameter estimates.

Model limitations

One of the primary assumptions underlying this model is that trawlers can, on an annual basis, control the relative proportions of the individual rockfish species in the catch. That appears to be a reasonable assumption for widow rockfish, which are caught primarily in a directed midwater trawl fishery. Catches of other rockfish species should be low in a midwater trawl fishery for shortbelly rockfish (Lenarz 1980), and the Pacific Fishery Management Council is unlikely to permit a bottomtrawl fishery for that species. Peak abundance of splitnose rockfish is in deeper water than for the other species used in this model; however, some

catches (particularly in the 100–149 fm depth interval) would likely contain bocaccio and chilipepper as well (Gunderson and Sample 1980). The greatest degree of overlap would be for bocaccio and chilipepper. Bocaccio occur over a greater latitudinal range than chilipepper, but in the area off California where both species are abundant, it could be difficult to maintain markedly different catch levels for the two species. An improved version of this model would incorporate probabilities for different levels of bycatch, so that the optimal policies would be constrained by the degree of targeting that was feasible (Pope 1979).

Another important assumption is that the species included in the objective function are interchangeable in the marketplace. That is a valid assumption for the commerically important *Sebastes* species, including widow rockfish, bocaccio, and chilipepper. However, demand for splitnose rockfish has been low because of its small size and low fillet yield (Lenarz 1986). A low price would be expected for shortbelly rockfish because they are small in size and must be processed rapidly (Lenarz 1986). Lenarz (1986) suggested that better marketing approaches will be needed before significant quantities of either splitnose or shortbelly rockfish can be harvested. For the model used in this study, differences in price among species could be accommodated easily and the objective function could be modified to maximize some function of income. It would also be of practical importance to determine whether all vessels participating in these fisheries caught all the species used in the objective function. Policies that result in variable catches of the species used in the model would be less appropriate if some fishermen did not catch or were unable to market some of the species.

The objective function could also be modified to include costs of fishing (see, for example, Pikitch 1987). However, the current practice of the Pacific Fishery Management Council is to manage for maximum sustainable yield; costs of fishing are not considered. Stock assessments are restricted to estimation of Acceptable Biological Catch (ABC), and the Council considers some socioeconomic factors when determining "Optimum Yield" from the ABC.

A limitation of this study was the assumption that model parameters M, B_∞, and A were known. Those parameters strongly affect equilibrium yields; consequently, when they are not well estimated, the passive policies used in this study might be outperformed by an adaptive probing strategy (Walters 1986). Under such a strategy, short-term fluctuations in fishing mortality and yield would be accepted in order to better estimate the productivity of the stock and improve long-term management.

Another potential limitation of the model used in this study was the assumption that errors in estimating biomass were not autocorrelated. That assumption may be valid when estimates are based on methods such as a swept-area trawl survey, although the fishery manager would be expected to balance any single estimate of stock size against observations from prior years. Autocorrelated errors would be likely in cases where estimates were based on a time-series of catch data. Such errors would be expected to have more serious consequences than the independent errors assumed here. An approach for introducing autocorrelated errors might be to use CVs of the same magnitude as assumed here but to use a 2- or 3-year moving-average estimate of biomass to set quotas. Errors in estimating biomass might also be correlated among species; for example, swept-area trawl surveys may underestimate the biomass of several species.

A possible limitation of this model was the assumption that the reliability of assessment data was equivalant for all species. If differences in the reliability of estimates were substantial, it might be found that a reliable single-species policy would be preferable to a multispecies policy that incorporated unreliable information on additional species.

Summary

1 When constant F policies for different objective functions were compared, the optimal F, total yield, and variance for total yield decreased as the level of risk aversion increased.

2 Single-species and multispecies variable F policies for maximizing harvest did not increase total yield significantly compared with constant F policies.

3 Single-species and multispecies variable F policies for the logh and negx objective functions provided a substantial reduction in the variance of total yield, compared with a constant F policy for maximizing harvest.

4 For the logh and negx objective functions, the variance for total catch was lower for the multispecies than for the single-species variable F policies, except for some cases for a five-species model or when biomass CVs were 50%.

5 Constant F policies for maximizing harvest (the current management approach) were essentially identical for different levels of random, non-autocorrelated errors in estimating biomass. Mean yield was slightly lower at higher biomass CVs for both constant F and variable F policies.

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Use of Otolith Microchemistry to Distinguish the Progeny of Sympatric Anadromous and Non-anadromous Salmonids

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Abstract.—Otolith microchemistry of anadromous and non-anadromous salmonids was investigated to determine if there were differences among migratory and nonmigratory individuals and if the habitat where vitellogenesis took place would affect the composition of the otolith primordia of the progeny. Electron microprobe transects across salmonid otoliths showed that there were large differences in otolith Sr/Ca ratios among adult anadromous and non-anadromous individuals, but there were no detectable differences in Na/Ca, K/Ca, and S/Ca ratios. The hypothesis that Sr/Ca ratios in the primordia of the progeny of anadromous salmonids would be greater than those in the primordia of the progeny of non-anadromous individuals because of differences in the composition of ova was tested and confirmed by the results of a controlled experiment. Also, the ova of anadromous *Oncorhynchus mykiss* were found to contain 5 times more Sr than their non-anadromous conspecifics. On the basis of these data, it was concluded that otolith nucleus Sr/Ca ratios can be used to distinguish the progeny of sympatric anadromous and non-anadromous salmonids.

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The ability to differentiate between juvenile anadromous salmonids and their sympatric non-anadromous conspecifics is essential for management of these species. However, stock discrimination between sea-run and resident freshwater salmonids has been limited to the adults upon their return from the sea to spawn. Furthermore, for those species where anadromy is a facultative, and not an obligate behavior, such as brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, Atlantic salmon *Salmo salar*, cutthroat trout *Salmo clarkii*, and Arctic char *Salvelinus alpinus*, it has been impossible to distinguish between the co-occurring forms on the basis of meristic or morphometric characters (Nordeng 1983, Jonsson 1985, Neilson et al. 1985). McKern et al. (1974) were able to distinguish between winter and summer races of steelhead trout (anadromous rainbow trout) from rivers in British Columbia, Washington, and Oregon on the basis of sagittal otolith nuclear dimensions that they believed to be affected by both qualitative and quantative differences in yolk. Rybock et al. (1975) concluded that differences in the size of female resident non-anadromous rainbow trout and steelhead trout resulted in differences in egg size and, subsequently, the size of the otolith nucleus in the progeny. However, both Neilson et al. (1985) and Currens et al. (1988) found that measurements of otolith nuclear dimensions were of questionable value in distinguishing juvenile non-anadromous and anadromous rainbow trout.

Development of ova in anadromous salmonids is virtually complete through vitellogenesis or yolk formation before the fish enter freshwater. On the basis of this information, I hypothesized that egg composition would, in some way, reflect the chemical composition of the seawater environment and that this would ultimately affect the composition of the otoliths of the progeny, particularly the otolith nuclei that are formed in the early stages of development and well before yolk utilization is complete. Yolk is formed through the deposition of a phospholipoprotein-calcium complex yolk precursor, vitellogenin, in the developing oocyte (Mommsen and Walsh 1988). Solubility and transport of vitellogenin through the circulatory system of the female and to the developing ovaries may be dependent on the presence of calcium which has been shown to increase markedly in female salmonids (Bailey 1957, Booke 1964, Elliot et al. 1979) and other fishes (Oguri and Takada 1967, Woodhead 1968) during gonad development. Vitellogenin has a high affinity for calcium due to the significant negatively-charged phosphate component of the molecule (Hara and Hirai 1978, Hara et al. 1980). The calcium binds to the vitellogenin molecule and, in this complexed form, the vitellogenin and calcium are deposited in

the oocyte. Clearly, yolk deposition is a conservative process in that the overall composition of the yolk is more dependent on the genetic programming of the female parent than the environment. However, in many calcium-binding proteins, such as vitellogenin, the calcium moiety of the complexed molecule can be substituted by strontium due to the similar structural features of Ca^{++} and Sr^{++} (Skoryna 1981). The relative degree of this substitution would be largely dependent on the relative concentrations of calcium and strontium in the ambient environment. Typical Sr/Ca ratios in marine waters (salinity 35‰) are 0.0087 (0.09 mM/kg Sr:10.3 mM/kg Ca) (Bruland 1983) and average 0.0019 (0.00068 mM/kg Sr:0.35 mM/kg Ca) in freshwater (Rosenthal et al. 1970). These differences would be expected to affect the Sr/Ca ratio of the yolk and, ultimately, the composition of the developing embryo and its otoliths.

In a study of otolith and endolymph composition, Kalish (1989) showed that the quantity of strontium incorporated into the otolith was directly related to the quantity of strontium present in the endolymph, and that anadromous brown trout collected in an estuary had higher levels of strontium in both the endolymph and otolith than non-anadromous brown trout. Therefore, it seems likely that differences in the elemental constituents of the yolk and embryos of anadromous and non-anadromous salmonids would result in differences in otolith composition. This hypothesis is supported by research that shows little or no exchange of calcium between prehatch salmonid embryos and the environment (Hayes et al. 1946, Zeitoun et al. 1976). This would be expected since calcium present in the yolk of the developing embryo is probably present in a protein-bound form and is destined for the tissues of the fry. Craik and Harvey (1984) found that the calcium composition measured in whole rainbow trout eggs was indistinguishable from the calcium measured in protein precipitate obtained from the egg. This, of course, excludes calcium that would be present in the fluid of the perivitelline space following fertilization (Laale 1980, Alderdice 1988). Strontium would probably behave similarly and there would be minimal loss of any seawater-derived protein-bound ions in the yolk to the freshwater environment where the development of salmonid embryos takes place.

In this paper, I discuss variations in the elemental composition of the otoliths of non-anadromous and anadromous salmonids with emphasis on the composition of the sagittal otolith nucleus. Several "life history" transects (scans of elemental composition across an axis of an otolith made with a wavelength-dispersive electron microprobe) are presented to indicate the variety of forms that these data may take in salmonids with differing life histories. I also present the results of an experiment designed to test the hypothesis that otolith primordia of the progeny of anadromous rainbow trout contain higher levels of strontium than the otolith primordia of non-anadromous rainbow trout. These data are examined in view of their usefulness in distinguishing the progeny of sympatric non-anadromous and anadromous salmonids and in investigations of diadromous behavior.

Methods

Brown trout (non-anadromous *Salmo trutta*) and sea trout (anadromous *Salmo trutta*) were collected by gillnet from the Derwent River and estuary, southeast Tasmania, Australia. Juvenile and adult rainbow trout were obtained from both wild and hatchery stock. Atlantic salmon were obtained from hatcheries. Otoliths were removed from fresh fish, cleaned, and stored in glass vials. Details of otolith preparation and microprobe analyses are described below.

Ripe ova were obtained from ovulating freshwater rainbow trout and sea-farmed rainbow trout and frozen in plastic bags for later analyses of calcium and strontium. Whole rainbow trout eggs were used for the determinations. Groups of 10 eggs from 4 freshwater and 4 sea-farmed trout were used. Preparation of eggs was modified from the methods employed by Craik and Harvey (1984). All solutions were made up with Milli-Q water (Millipore Corp.). Groups of eggs were weighed wet and then oven-dried at 50°C for 24 hours to estimate dry weight. The dried whole eggs were ashed at 500°C for 24 hours and then digested in 2.0 mL Aristar ultrapure hydrochloric acid at 100°C for 2 hours. Samples were separated into two equal aliquots for separate calcium and strontium determinations. Sample digests for estimation of calcium were diluted in 10 mM lanthanum chloride to suppress interference due to phosphate binding. Calcium concentrations were determined by flame atomic absorption spectrophotometry using an air-acetylene flame.

Strontium concentrations in eggs were determined by the method of standard additions using graphite furnace atomic absorption spectrophotometry on a Varian AA-1475 spectrophotometer equipped with a GTA-95 graphite furnace and an autosampler. Argon was used as the purging gas in the graphite furnace. Samples were diluted with a 0.25% solution of an ionic detergent, Triton X-100, and 20 μL of diluted sample were injected by autosampler into a walled, pyrolytically coated graphite tube. Furnace conditions were: drying

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Electron microprobe analytical data for salmonid otolith analyses. Details of counting times, counting precision, and materials used as standards. Calculation of the counting precision is discussed in Goldstein et al. (1981). Precision values are for the 95% confidence level.

Spectrometer/ crystal	Element	Peak counting time (sec)	Counting precision	Standard material	Source
1/PET	Ca-K_α	10	~28,000 counts collected 1.0%	Calcite	USNM* 136321 Jarosewich and MacIntyre (1983)
1/PET	K-K_α	30	15% when K/Ca = 2×10^{-2}	Anorthite	USNM 137041 Jarosewich et al. (1980)
2/PET	S-K_α	40	36% when S/Ca = 1×10^{-3}	Troilite	BMR** Museum Ramdohr and Goresy (1971)
3/TAP	Na-K_α	20	8.1% when Na/Ca = 2×10^{-2}	Anorthite	Same as for K above
3/TAP	Sr-L_α	20	9.9% when Sr/Ca = 3×10^{-4}	Strontianite	USNM 10065 Jarosewich and White (1987)

*Natl. Mus. Nat. Hist., Smithsonian Inst., Wash., DC
**Bur. Miner. Resour., Canberra, Australia

at 90°C for 60 seconds; ramp ashing from 90 to 700°C for 20 seconds; ashing at 2600°C for 1 second; and atomization, with no gas flow, at 2600°C for 3 seconds.

To confirm the hypothesis regarding otolith nucleus composition, eggs were obtained from sea-farmed and freshwater broodstock rainbow trout which originated from a similar hatchery stock (Cressy, Tasmania). These two groups of hatchery fish derive from similar stocks of rainbow trout imported into Tasmania; because of minimal gene flow, inbreeding is relatively great and the diversity of the gene pool is low. Both freshwater and sea-farmed adults had been maintained on jack mackerel *Trachurus declivis* based pellets throughout the period of egg development. Sea-farmed broodstock were kept at the same hatchery as freshwater broodstock for 3 weeks before stripping, and all eggs were fertilized with sperm from a male of freshwater stock. The developing embryos from sea-farmed and freshwater broodstock were maintained in separate baskets in the same channel of a recirculating water system where temperature was maintained at 10°C. A natural photoperiod was maintained throughout the experiment. A random sample of 20 freshwater progeny and 20 sea-farmed progeny was taken 20 days after hatching, and these fish were frozen for later removal of otoliths. Sagittae and lapilli were removed from fry, the adhering otolith capsule was removed, and otoliths were rinsed in deionized water. Otoliths were oven-dried at 40°C. The length of sagittae and lapilli was measured with an ocular micrometer.

Otoliths from adults were embedded in Araldite D epoxy resin (Ciba-Geigy) and polymerized in an oven at 40°C for 48 hours. Several transverse sections of approximately 200 μm thickness were obtained from otoliths, including one section containing the primordium, with a low-speed saw (Struers Accutom) equipped with a diamond cut-off wheel. Sections were affixed to glass slides with epoxy. After drying, sections were ground with a graded series of carborundum paper (wet/dry paper 600–1200 grade) until the primordia were reached. The much smaller otoliths from fry were mounted, sulcus-side-up, in Crystalbond 509 (Aremco Products, Inc.), a heat-labile thermoplastic polymer (Neilson and Geen 1981), and ground in the sagittal plane to the level of the primordia with 1200-grade wet-dry paper. All otoliths were then ground to the precise level of the primordia on a lapping wheel with 0.25 μm aluminium paste (Linde A) and then finished with 0.25 μm diamond paste. Polished specimens were ultrasonically cleaned in reagent-grade mineral spirits followed by ultrasonic cleaning in deionized water and oven drying at 60°C. Samples were then coated in a high-vacuum evaporator with a 25-nm carbon layer and stored in a dessicator.

Otolith elemental analyses were carried out with a Cameca SX-50 wavelength-dispersive electron microprobe. Analyses were made with a square raster of 10×10 μm. Probe current and accelerating voltage were 10 nA (measured on Cu) and 15 kV, respectively. Elements analyzed included Ca, Sr, Na, K, and S. Salmonid otoliths are very susceptible to damage from the electron beam, and it was necessary to utilize a low-beam current and reduced counting times for all analyses. In conjunction with these conditions that reduce the total number of X-ray counts from a specimen, it is important to be aware of detection limits and counting statistics. A treatment of these subjects can be found in Goldstein et al. (1981) and references therein.

Details of the microprobe counting procedures, precision, and standards employed in this study are outlined in Table 1. Background was measured at offsets both above and below peak position for 50% of the peak counting time. The average counts from these two background measurements were subtracted from the peak. Background measurements were made with each analysis. Corrected X-ray intensity ratios were calculated using the ZAF method (Reed 1975), and the final elemental ratios are normalized atom ratios based on concentrations derived from the standards.

Elemental data for otolith life-history transects from adult salmonids were collected with approximately 40 μm separating each 10×10 μm sample region (50 μm separating the center point of each sample). This sampling spatial frequency was judged to be adequate because it was desired to collect data relating to major life-history changes only, and not recurring or seasonal events.

For a comparison of otolith composition among the progeny of sea-farmed fish and freshwater fish, microprobe data were collected from five individual primordia within each sagitta or lapillus. In some lapilli it was necessary to make multiple measurements on individual primordia because five primordia were not always exposed or visible. In addition, five microprobe measurements were made on each otolith at points near the otolith edge that were indicative of the otolith composition at a time after the completion of yolk absorption.

Results

Otolith life-history transects representative of several types of adult salmonids are presented in Figure 1. Differences in otolith transects among anadromous or sea-farmed fish and non-anadromous individuals are only evident in the Sr/Ca data and, therefore, only Sr/Ca life-history transects are presented. Sea trout, sea-farmed Atlantic salmon, and sea-farmed rainbow trout exposed to the marine environment display a clear increase in otolith Sr/Ca that is coincident with entry into seawater.

There is an initial peak, associated with the otolith nucleus, in the Sr/Ca ratio of the sea trout and Atlantic salmon, but this peak does not appear in the sea-farmed or freshwater rainbow trout. In Tasmania, freshwater broodstock are used for the production of sea-farmed rainbow trout. The peak in otolith Sr/Ca in the otolith nucleus of some individuals is presumably due to the presence of strontium sequestered in the egg yolk proteins during the seawater phase of ovarian development of the fishes' female parent.

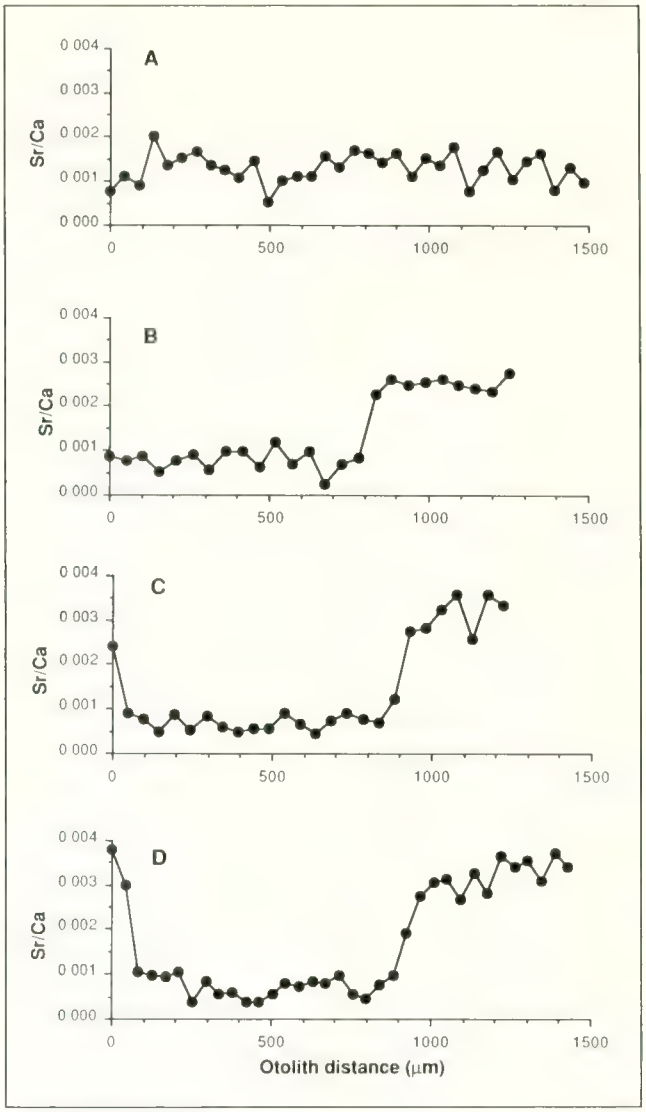

Figure 1

Transects of otolith Sr/Ca ratios measured with a wavelength dispersive electron microprobe from the primordium (0 μm) to the otolith edge along transverse sections of sagittae from 4 female adult salmonids with differing life histories. Each point represents a single measurement made over an area of 100 μm^2. (A) Wild non-anadromous *Oncorhynchus mykiss* from Great Lake, Tasmania; (B) sea-farmed *Oncorhynchus mykiss*; (C) sea-farmed *Salmo salar*; and (D) wild anadromous *Salmo trutta* from the Derwent River estuary.

The hypothesis that the seawater strontium contribution to the egg would result in increased otolith strontium was confirmed by the results of the rearing experiment. Results of this experiment are presented in Table 2. Mean Sr/Ca ratios based on measurements in five primordia from each of the 20 sea-farmed broodstock progeny was 0.00313 ± 0.00068, significantly greater than the mean value of 0.00114 ± 0.00014 measured in the primordia of the freshwater brood-

Table 2

Mean elemental ratios measured in primordia and post-yolk absorption regions in the sagittae and lapilli of progeny of sea-farmed and freshwater rainbow trout *Oncorhynchus mykiss*. Values are means ±1 standard deviation based on 5 microprobe measurements in the nucleus and post-yolk absorption regions of each otolith. $N = 20$ for sagittae, and $N = 5$ for lapilli. Significance tests alongside sagittae and lapilli primordia data are the results of paired two-tailed t-tests between those otolith primordia and the post-yolk absorption regions of the same otoliths.

	Sr/Ca ($\times 10^3$)	Na/Ca ($\times 10^2$)	K/Ca ($\times 10^1$)	S/Ca ($\times 10^1$)
Sea-farmed progeny				
Sagittae ($N = 20$)				
Primordia	3.13 ± 0.68***	2.03 ± 0.16***	2.07 ± 0.47***	1.65 ± 0.63**
Post-yolk absorption	1.07 ± 0.31	1.86 ± 0.16	2.62 ± 0.52	1.08 ± 0.21
Lapilli ($N = 5$)				
Primordia	4.34 ± 0.80**	1.98 ± 0.09*	1.84 ± 0.30*	1.30 ± 0.35 ns
Post-yolk absorption	0.83 ± 0.24	1.74 ± 0.06	2.30 ± 0.07	1.00 ± 0.14
Freshwater progeny				
Sagittae ($N = 20$)				
Primordia	1.14 ± 0.14 ns	2.10 ± 0.08***	2.61 ± 0.41 ns	1.75 ± 0.38***
Post-yolk absorption	0.96 ± 0.19	1.73 ± 0.15	2.46 ± 0.37	1.21 ± 0.21
Lapilli ($N = 5$)				
Primordia	1.20 ± 0.18 ns	1.95 ± 0.04*	2.43 ± 0.25 ns	1.32 ± 0.14 ns
Post-yolk absorption	1.06 ± 0.13	1.72 ± 0.06	2.68 ± 0.26	1.27 ± 0.27

*$P \leq 0.01$; **$P \leq 0.001$; ***$P \leq 0.0001$; ns = not significant ($P > 0.05$).

stock progeny (unpaired one-tailed t-test, $t = 12.69$, $P < 0.0001$). One-way analysis of variance showed that there were no significant differences in mean otolith primordia Sr/Ca ratios among individuals from either seawater ($F = 0.88$, $P = 0.476$) or freshwater broodstock ($F = 1.29$, $P = 0.279$). Differences in otolith primordia composition between sea-farmed progeny and freshwater progeny were not significant for Na/Ca (unpaired two-tailed t-tests, $t = 1.82$, $P = 0.076$) and S/Ca ($t = 0.58$, $P = 0.568$), but were significant for K/Ca ratios ($t = 3.88$, $P = 0.0004$). Similar results were obtained for measurements made in lapilli primordia from five freshwater and five marine progeny. Table 2 also presents the results of comparisons between the composition of the nucleus and post-yolk absorption regions of the otoliths.

A histogram of the frequency distribution of Sr/Ca ratios determined for five primordia in the sagittae of 20 progeny of sea-farmed rainbow trout and 20 progeny of freshwater rainbow trout shows that there is little overlap between individual measurements from the two groups (Fig. 2). Only 5% of the measurements from the sea-farmed progeny overlap with 13% of the freshwater progeny measurements. A frequency histogram of the mean Sr/Ca ratios obtained from each sagitta nucleus shows that the sea-farmed and freshwater progeny are clearly separated on the basis of otolith primordia Sr/Ca ratios (Fig. 2).

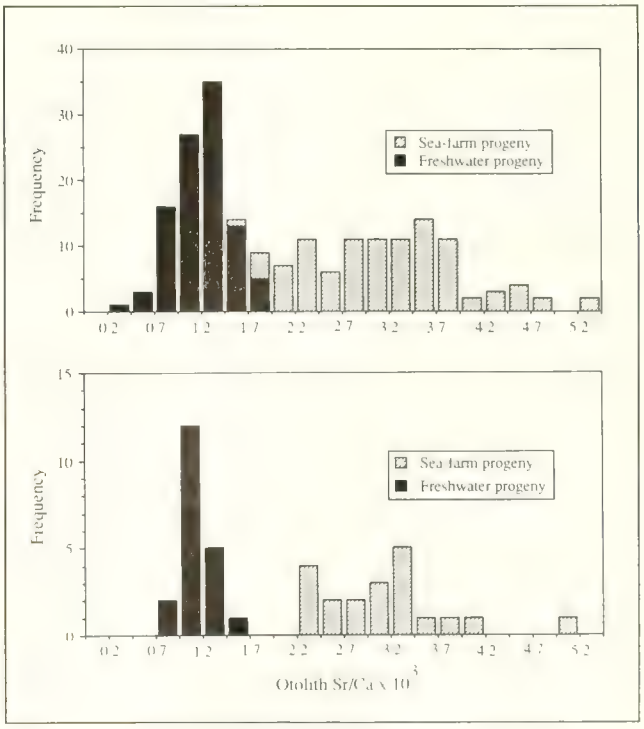

Figure 2

(Above) Frequency distribution of individual otolith Sr/Ca measurements made in the primordia of 20 sagittae from *Oncorhynchus mykiss* fry of sea-farmed broodstock and 20 sagittae from fry of freshwater broodstock ($N = 200$), and (below) frequency distribution of mean otolith Sr/Ca ratios from the same 40 sagittae.

Measurements of otolith composition made in regions of the sagittae formed after the completion of yolksac absorption and corresponding with a period soon after first feeding corroborated data that showed the influence of yolk on otolith composition. There were no significant differences in Sr/Ca (unpaired two-tailed t-tests, $t = 1.30$, $P = 0.201$), S/Ca ($t = 2.02$, $P = 0.051$), or K/Ca ($t = 1.09$, $P = 0.282$) ratios measured in the later-formed regions of the otoliths from the two groups of fry and only slightly significant differences for Na/Ca ratios ($t = 2.70$, $P = 0.010$). Differences between the Sr/Ca ratio of the sagitta edge and primordium were highly significant in the sea-farmed broodstock progeny (paired two-tailed t-tests, $t = 10.38$, $P < 0.0001$), and only slightly significant in the progeny of the freshwater broodstock ($t = 3.13$, $P = 0.003$).

Six electron microprobe transects over a sagitta from a single *Oncorhynchus mykiss* fry of sea-farmed broodstock origin were made to show Sr/Ca ratios over the entire otolith including the nucleus and pre- and post-yolk absorption regions (Fig. 3). The outermost points towards the otolith rostrum and posterior show the sagitta Sr/Ca ratios after the completion of yolksac absorption and provide evidence for much reduced otolith Sr/Ca ratios when compared with the otolith material produced during the period of yolksac utilization. The data also indicate that, in general, high Sr/Ca ratios prevail throughout the region of the nucleus and are not confined to the primordia alone.

Measurements of egg calcium and strontium composition show that ova of the sea-farmed rainbow trout contain higher levels of strontium than their freshwater conspecifics. The mean strontium content was 0.054 ± 0.013 μM/g of ova (dry weight) for ova that had developed in seawater and 0.010 ± 0.002 μM/g for ova from freshwater fish, and the difference between these values was significant (unpaired two-tailed t-test, $t = 6.60$, $P = 0.0006$). Mean calcium content of yolk was 0.035 ± 0.005 mM/g from sea-farmed broodstock and 0.026 ± 0.004 mM/g from freshwater fish and these values were also significantly different ($t = 3.06$, $P = 0.022$).

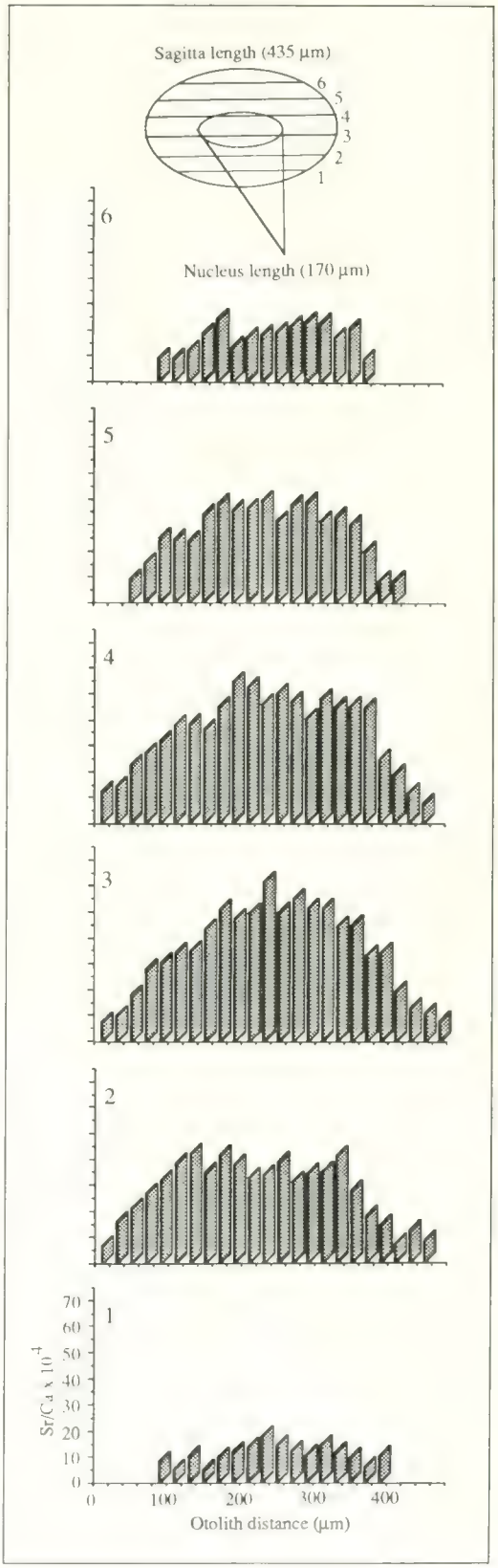

Figure 3

Six transects of otolith Sr/Ca ratios made with a wavelength-dispersive electron microprobe on a single sagitta from a 60-day-old fry of sea-farmed trout stock origin. The otolith was ground to the level of the primordia in the sagittal plane. Each column in the histograms represents an individual microprobe measurement ($N = 120$). Outermost points show the sagitta Sr/Ca ratios after the completion of yolksac absorption.

Discussion

The results present evidence that the Sr/Ca ratios of otolith primordia formed during embryonic development are directly influenced by the strontium content of the individual's yolk and that yolk composition is also influenced by the composition of the waters where vitellogenesis took place. These findings are important to the study and management of salmonid species where anadromy is a faculative behavior. They may also be important to studies of other diadromous species, but it remains to be seen whether the relatively small nutritive contribution of the yolk in these fishes is adequate to influence otolith composition. However, since otolith primordia develop very early in the ontogeny of fishes (Brothers 1984), there may be detectable differences in otolith strontium content within other species that display facultative diadromy. In many cases, the analysis of otolith primordium composition should make it possible to investigate the relative importance of parentage and environment in determining diadromous behavior.

The basis for the differences in otolith primordium composition among anadromous and non-anadromous fishes is such that there is probably little, if any, effect of race or population. Both wild and hatchery salmonids involved in this study displayed similar ranges of elemental ratios, depending on habitat (freshwater or marine) indicating that different salmonid species may incorporate into their otoliths a similar proportion of the ions present in the endolymph. Furthermore, this indicates that the relationship between endolymph and blood plasma composition is regulated in a similar manner in each of these species. Kalish (1989) showed that there was a tendency for both endolymph and otolith Sr/Ca ratios to be similar among individuals of a species, whereas differences were greatest among species. On the basis of the data presented here and in Kalish (1989), it seems likely that freshwater and marine salmonid otolith Sr content could be predicted on the basis of endolymph composition.

The results of this study confirm that differences in the composition of freshwater and seawater can be reflected in the composition of fish otoliths. These findings are similar to those obtained by Casselman (1982), Radtke et al. (1988), and Kalish (1989). Wavelength-dispersive electron microprobe analyses of strontium content in diadromous fish otoliths can provide information on the rates of migration to and from the sea, residence times at sea and in freshwater, the age at which migrations take place, and confirmation of data obtained from scales.

Confirmation of data obtained from scale reading is important because of the possibility of scale resorption (Bilton 1974) and the equivocal nature of data obtained from scales in the discrimination of adult anadromous and non-anadromous salmonids. Bagenal et al. (1973) used the strontium content of whole scales to distinguish between brown trout and sea trout, and Moreau and Barbeau (1979) used a similar rationale to discriminate anadromous from non-anadromous whitefish *Coregonus clupeaformis*. However, Castonguay and FitzGerald (1982) found that this method was unreliable for distinguishing between anadromous and non-anadromous brook char *Salvelinus fontinalis*, and Gausen and Berg (1988) had similar results when investigating migratory and non-migratory Atlantic salmon. Measurements of otolith Sr may provide a more reliable means of determining migratory behavior in these species because otoliths are not resorbed during periods of stress (Simkiss 1974, Campana 1983), although Mugiya and Uchimura (1989) present evidence for otolith resorption in goldfish *Carassius auratus* during extreme anaerobic stress. Also, otolith Ca and, most likely, Sr are derived from ions taken up by the gills (Simkiss 1974), and any variations in the Sr content of the diet would not be reflected in the composition of the otoliths. This is not the case for scales, and differences in the Sr content of the diet as well as the effect of different levels of discrimination against Sr would be manifested in scale composition.

It is important to point out the inadequacy of energy-dispersive (ED) electron microprobe analysis for the determination of Sr at the levels typically found in marine fish otoliths and particularly in the otoliths of freshwater species. Under optimal operating conditions, the minimum detectability limit for a wavelength-dispersive (WD) electron microprobe is approximately 10 times lower than that of an ED microprobe for all elements (Geller 1977, Goldstein et al. 1981). Generally, the minimum detection limits attainable with an ED spectrometer are on the order of 0.10% wt (1000 ppm), and these conditions are frequently not realized due to various factors. The range of Sr concentrations measured in this study was approximately 300–5000 ppm, and all marine fish otoliths investigated to date appear to contain Sr in excess of 1000 ppm (Radtke 1987, Edmonds et al. 1989, Kalish 1989). Theoretically the ED spectrometer should be capable of making all otolith Sr measurements in marine fish and some of those from freshwater fish. However, the detection and accurate quantitative estimation of Sr creates special problems for the ED microprobe.

The X-ray line that is used to detect Sr at 1.806 keV (L_α) is affected by the silicon escape peak associated with the large Ca K_α peak produced when measuring specimens that are largely calcium (aragonite fish otoliths are approximately 38% wt Ca). The silicon escape peak results from the production of Si K_α photons following absorption of relatively high energy (>1.841

keV) photons by the silicon detector of an ED spectrometer (Reed and Ware 1972). The energy of the photon producing the escape peak is $E_x - E_{Si}$, where E_x is the incident photon energy and E_{Si} is the energy of a Si K_α photon (1.739 keV). The silicon escape peak due to Ca K_α would have an energy of 1.951 keV (3.690 keV − 1.739 keV) and an intensity 0.78% that of the Ca K_α peak (Reed 1975). Such a peak, within less than 150 eV of the Sr peak, would create significant errors in the estimation of low levels of Sr. Measurements of trace levels of phosphorus with the K_α line (2.013 keV) would be even more vulnerable to errors because of the closer proximity to the Ca K_α derived silicon escape peak. Other errors can result from a silicon internal fluorescence peak (Reed and Ware 1972) and the silicon absorption edge (Goldstein et al. 1981, Statham 1981), both artifacts of the ED spectrometer and associated silicon detector, and of particular interest to the determination of trace levels of Sr. These sources of error are not present when using a WD electron microprobe.

There are numerous other potential sources of error in otolith trace-element studies carried out with ED electron microprobes. These errors can occur due to the relatively poor energy resolution of the ED spectrometer and the resultant inability to discriminate between X-ray lines separated by less than approximately 150 ev (Statham 1981). Furthermore, the presence of a greater proportion of continuum background radiation or "bremsstrahlung" in the ED spectrometer, due to decreased energy resolution, results in a fivefold increase in the peak to background ratio in a WD spectrometer over an ED spectrometer (Reed 1975). These factors, and others, make it necessary to view with caution studies with ED microprobes that investigate the distribution of large numbers of trace (<0.5% wt) elements, particularly without reference to criteria for determining detection levels or precision. In an investigation of otolith composition using X-ray fluorescence spectroscopy (XRF) Cu, Cd, Cr, and V were below the detection limits of the instrument (<3.0 ppm), Ni was found at levels averaging 2.0 ppm, and Fe, Zn, and Ba levels were below 10 ppm in the four species studied (J.M. Kalish, unpubl. data). Edmonds et al. (1989) used inductively coupled plasma atomic-emission spectroscopy (ICP—AES) to study otolith composition of the pink snapper *Chrysophrys auratus* for stock discrimination, and their data indicate that Mg, Si, and Fe are at levels below the detection limits achievable using either ED or WD microprobe analysis.

With the above results in mind it appears that with a WD electron microprobe the only elements that can be reliably quantified in otoliths are Ca, Na, Sr, K, S and, in some cases, Cl. However, in the case of Cl, the presence of this element in the most frequently used mounting medium, epoxy, makes the quantitative determination of this element difficult. If it is desired to detect Cl, an alternative mounting medium should be considered. The utility of ED microprobe analysis to studies of the quantitative composition of fish otoliths seems to be limited to Ca and, in some rare instances, Na and Sr.

Although WD microprobe analysis is generally capable of detecting the levels of Sr found in freshwater and marine fish otoliths, there are some limitations to the method in studies of anadromous fishes. Most important is the limited spatial resolution of the microprobe. In this study the probe size was maintained at 10×10 μm to minimize beam damage of the specimen. A spot of this size on the otolith of an adult fish would encompass more than a single day of otolith growth and in slow-growing individuals could encompass a month or more. In slow-growing fish, this would limit the ability to determine the temporal scale of migratory events. Determination of the temporal resolution of the microprobe data would be dependent on estimates of fish age based on otolith annuli and microincrement data. In many instances, the utility of otolith Sr data is dependent on the accurate determination of age using the same otolith.

The elemental analysis of otolith primordia should provide an objective criterion for assessing if an individual is the progeny of an anadromous or non-anadromous female. This information alone, or in combination with data from life-history transects, should make it possible to investigate the relationships between genetics and environment on diadromous behavior and aid in the management of species that display faculative diadromy. However, as with any new method, it is important to confirm the validity of these results for the particular species and habitat in question.

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Abstract.—Density and biomass estimates from a shrimp trawl and a visual survey are compared. Results indicate that the visual survey gives estimates eight to nine times larger than the trawl survey. However, there are important variations by species. Estimates of fish size from the visual censuses are larger than fish sizes observed in the trawl catch. These results suggest that the catchability of fish by shrimp trawls may be lower than usually thought for multispecies tropical stocks. In shrimp trawl fisheries, this may have important consequences for stock assessment and for evaluation of parameters such as fishing mortality. Trawling should be adequate for qualitative and semiquantitative stock assessment, but will need to be compared with other methods for quantitative studies on multispecific stocks.

Comparison Between Fish Bycatch from Shrimp Trawlnet and Visual Censuses in St. Vincent Bay, New Caledonia

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Shrimp trawl fisheries are the source of a large fish bycatch in the tropical Indo-Pacific (Aoyama 1973, Grantham 1980, Villoso and Hermosa 1982, Chong 1984). One question concerning these fisheries is how much damage they cause to fish stocks. To answer this question, it is useful to assess the catchability of fish by shrimp trawls. Many methods exist to assess this parameter. Most use the same gear under different conditions, such as double codends, split codends, and replicate hauls with different mesh sizes (Macket 1973, Gulland 1975). The bias of such methods may be acceptable for single-species populations but has seldom been studied in relation to tropical multispecies stocks. Another approach is the cross-evaluation of trawling and echosurveys (Doubleday 1976, Dines 1982, Dickie et al. 1983), but this method is not well adapted to tropical multispecies stocks. Another way is to correlate the results of two methods, such as with a TV camera and otter trawl (Uzmann et al. 1977), submersible and longlines (Ralston et al. 1986, Richards and Schnute 1986, Grimes et al. 1982), visual census and longlines (Kulbicki 1988) or poisoning and beamtrawl (Gray and Bell 1986).

The use of several methods has the advantage of allowing some evaluation of the biases of each method. In the present study it was possible to compare the results of visual censuses and shrimp trawl bycatches. This work was originally designed to estimate the catchability of the net (q = number of fish caught/number of fish present), but it also provided information on the biology of the fish.

Material and methods

Location

The study was performed during August 1986 on the trawling grounds of the South Bay in St. Vincent Bay, in the southwest lagoon of New Caledonia. The trawling grounds cover 15 km^2, or approximatively one-tenth of the Bay area. A total of eight stations were sampled (Fig. 1), one of which was sampled at night (Station n°6).

Visual census

A 200-m transect line was laid on the bottom with a buoy set at each end of the line. The transect was divided into 10-m sections. For each section, two divers—one on each side of the line—counted all fish, estimated their length, and estimated the perpendicular distance of the fish to the transect. Length was given in 2-cm size classes for fish less than 20 cm, 5-cm size classes for fish between 20 and 50 cm, and 10-cm size classes for fish larger than 50 cm. Only fish less than 1.5 m above the bottom were counted. The distance from the fish to the transect was recorded in 1-m

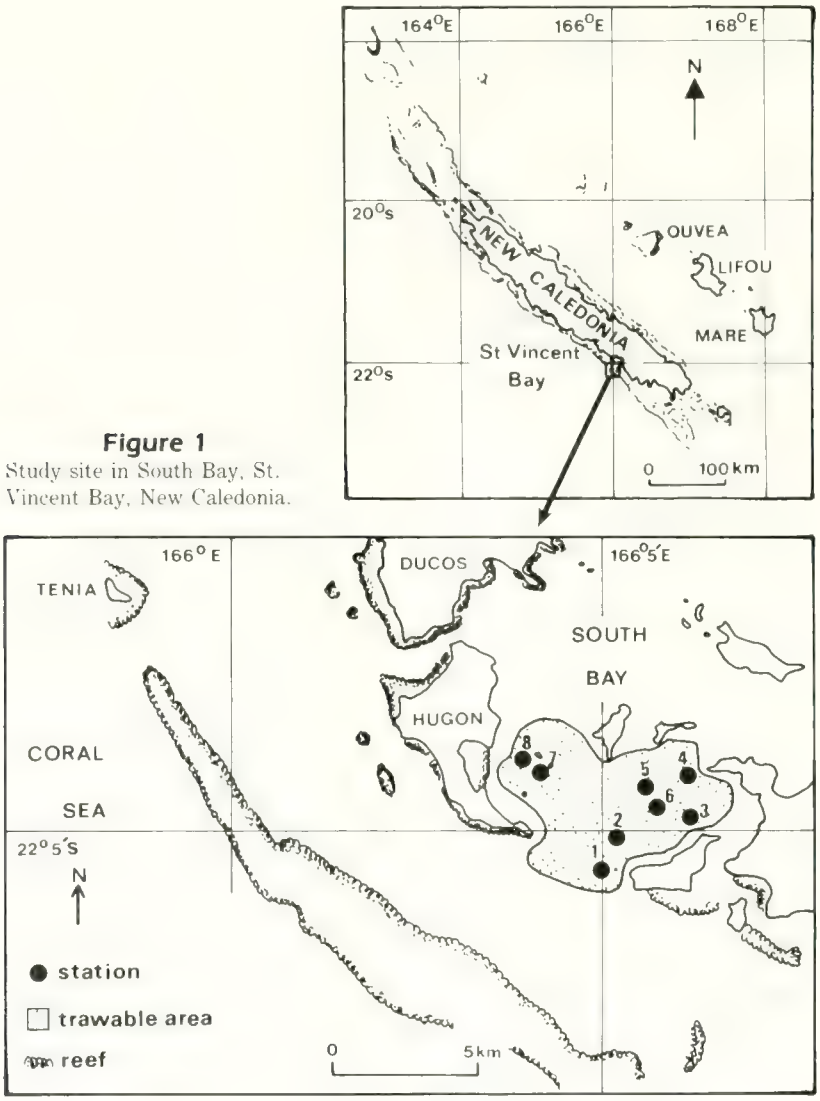

Figure 1
Study site in South Bay, St. Vincent Bay, New Caledonia.

classes up to 5 m, and in 2-m classes beyond 5 m. Fish were not recorded beyond 10 m from the transect. Both divers had a good knowledge of the fish fauna and also had a good training in visual censuses. The transects were finished between 30 and 45 minutes before the start of the trawling.

For this type of data, many density estimators may be chosen (Burnham et al. 1980). Among these estimators, Kulbicki and Duflo (unpubl. data) show that the most robust one for fish density (D) in similar conditions is given by:

$$D = (10^4/2L) \sum_{i=1}^{p} (n_i/d_i)$$

where D = fish density (fish/ha),
p = number of species,
n_i = number of fish of species i,
d_i = average distance (m) of species i to the transect, and
L = length of the transect (200 m).

Biomass B (kg/ha) was calculated in a similar fashion:

$$B = (10/2L) \sum_{i=1}^{p} (w_i/d_i)$$

where w_i = weight of species i (g).

The weights of fish were estimated from length-weight relationships (Wantiez and Kulbicki In press).

Trawling

The RV *Vauban* (24 m long) towed a shrimp trawlnet of the semiballoon, floridian type with a 14-m headrope and a 2-cm mesh codend. The vertical opening was 1.2 m and the distance between the otterboards was 7 m at a speed of 2 knots. Towing speed varied from 2 to 2.5 knots.

The hauls were each 800 m in length (±80 m). The net was submerged immediately after completion of the visual census at a distance of 400 m from the first buoy of the transect. The track of the haul was along the transect line and the net was retrieved 200 m after the second buoy of the transect line. All fish caught were sorted to species (Rivaton et al. 1990). All fish were counted and weighed.

For the calculation of density D (fish/ha), no catchability coefficient was used. Therefore,

$$D = \sum_{i=1}^{p} (n_i/S)$$

where p = number of species caught,
n_i = number of fish of species i, and
S = surface area of the haul (7 m × 800 m = 5600 m^2 = 0.56 ha).

Biomass (kg/ha) B was estimated in a similar fashion,

$$B = \sum_{i=1}^{p} w_i/S)$$

where w_i = weight of species i (kg).

Results

Species

A total of 82 species were either caught by trawls or recorded by divers (Table 1). All the common species known to occur in trawls in St. Vincent Bay (Kulbicki and Wantiez 1990) were found in the present study except for the Leiognathidae (ponyfishes). This family, represented by eight species in the bay, is characterized by large fluctuations in trawl catches depending on season and locality. In the present survey, *Leiognathus rivulatus* which is normally an uncommon species in the catch, was the major Leiognathidae.

Table 1 indicates that the trawls caught more species (64) than were seen on the transects (51). This could be due to the larger area covered by the trawls (~5600 m^2/trawl versus 700–1000 m^2 per transect). Most cryptic species, such as Scorpaeniforms, Platycephalidae (flatheads), flatfishes, and small Balistidae (triggerfishes) (including the filfishes *Paramonacanthus japonicus* and *Pseudalutarius nasicornis*) were poorly represented in the visual transects but caught by the trawls. Conversely, small species such as Apogonidae (cardinalfishes) and Pomacentridae (damselfishes) could be detected on the transects but were too small to be retained by the net. Large, fast-swimming species such as Carangidae, Serranidae, or Scombridae were seen on the transects but evaded the trawls. Gobiidae, which are burrowing species, were also seen during the dives but absent from the trawl catch.

A total of 32 species were detected by both methods (Table 1). Among these, only eight species were seen or caught in more than 50% of the samples for both methods (*Saurida undosquamis*, *Synodus hoshinonis*, *Leiognathus rivulatus*, *Lethrinus nematacanthus*, *Upeneus tragula*, *Upeneus* sp. aff. *asymetricus*, *Pristotis jerdoni*, and *Canthigaster compressa*). These eight species will subsequently be referred to as "main species." Except for *Synodus hoshinonis* and *Leiognathus rivulatus*, all these fish are among the 15 most frequent species in the trawl catch of St. Vincent Bay (Kulbicki and Wantiez 1990).

The number of species per station was statistically larger (t test at $\alpha = 0.05$) for the trawls than for the transects (Table 2). However, a chi-square test for independent samples (Siegel and Castellan 1988) indicates that the ranking of the stations is not significantly different (at $\alpha = 0.05$) between methods.

Fish size

Only fish lengths were used to compare fish size between the two methods. Table 3 indicates that visual censuses always yielded larger lengths than trawls, except in the case of *Pristotis jerdoni*. However, the lengths are significantly different (t test at $\alpha = 0.05$) for only four species (Table 3), and the two methods give mean lengths which are less than 2.8 cm apart. Due to the fact that fish length was estimated in 2-cm size classes for transects and 0.5-cm size classes for trawls, one should be cautious about the significance of the differences observed.

In a review on the problems of visual transects, Harmelin-Vivien et al. (1985) indicate that fish size is usually underestimated by this method. In the present study, if this were the case, it would mean that the larger fish (within a given species) are able to evade the trawl. In our opinion this is not the only reason, and the discrepancy of fish length between transects and trawls is probably also due to an overestimate of length by the divers.

Table 1

Species composition of transects and trawls in St. Vincent Bay, New Caledonia. For dives and trawls, numbers indicate at how many stations the species were recorded.

Species	Dives	Trawls
Muraenidae		
Muraenidae spp.	1	4
Synodontidae		
Saurida gracilis	0	2
Saurida nebulosa	0	2
Saurida undosquamis	4	4
Synodus dermatogenis	1	0
Synodus hoshinonis	4	7
Trachinocephalus myops	0	1
Carapidae		
Carapus homei	0	1
Fistularidae		
Fistularia petimba	0	1
Syngnathidae		
Hippocampus histrix	0	1
Dactylopteridae		
Dactyloptena orientalis	0	2
Scorpenidae		
Scorpaenidae sp.	0	1
Dendrochirus brachypterus	0	1
Pterois volitans	1	0
Synanceiidae		
Inimicus didactylus	0	3
Aploactinidae		
Aploactis aspera	0	2
Platycephalidae		
Platycephalidae spp.	1	7
Onigocia spinosa	0	3
Serranidae		
Cephalopholis boenack	2	0
Epinephelus cyanopodus	2	0
Epinephelus maculatus	3	0
Epinephelus malabaricus	0	1
Priacanthidae		
Priacanthus hamrur	0	2
Apogonidae		
Apogon spp.	2	1
Apogon catalai	0	1
Apogon ellioti	0	4
Apogon aureus	1	0
Apogon trimaculatus	1	1
Apogon sp. cf *compressus*	0	1
Cheilodipterus quinquelineatus	0	1
Rhabdamia spp.	1	0
Carangidae		
Decapterus russelli	1	2
Gnathanodon speciosus	1	0
Siganidae		
Siganus canaliculatus	0	3
Scombridae		
Scomberomorus commerson	1	0
Bothidae		
Asterolepis sp.	0	1
Asterorhombus intermedius	1	8
Engyprosopon grandisquama	1	7
Grammatobothus polyophthalmus	0	3
Balistidae		
Abalistes stellatus	0	3
Pseudobalistes flavimarginatus	1	7
Pseudobalistes fuscus	2	4
Leiognathidae		
Leiognathus rivulatus	5	6
Secutor ruconius	1	0
Lutjanidae		
Lutjanus quinquelineatus	2	2
Lutjanus vittus	2	3
Gerreidae		
Gerres oratus	1	3
Haemulidae		
Diagramma pictum	2	1
Lethrinidae		
Lethrinus nematacanthus	6	8
Lethrinus semicinctus	1	2
Nemipteridae		
Nemipterus peroni	0	2
Scolopsis temporalis	3	6
Mullidae		
Parupeneus pleurospilos	1	4
Upeneus sp.	0	1
Upeneus moluccensis	1	2
Upeneus tragula	7	7
Upeneus sp. aff. *asymetricus*	6	8
Chaetodontidae		
Heniochus acuminatus	1	1
Pomacentridae		
Chromis fumea	1	0
Dascillus aruanus	0	1
Neopomacentrus sp. Allen	1	0
Pristotis jerdoni	4	5
Labridae		
Anampses spp.	1	0
Cheilinus bimaculatus	2	6
Xiphocheilus typus	0	2
Scaridae		
Scarus ghobban	0	1
Mugiloididae		
Parapercis sp.	2	0
Parapercis cylindrica	1	2
Blenniidae		
Petroscirtes breviceps	2	1
Callionymidae		
Synchiropus ramulus	0	2
Gobiidae		
Gobiidae sp.	2	0
Amblyeleotris sp.	2	0
Amblygobius sp.	1	0
Ptereleotris hanae	1	0
Ostraciidae		
Tetrasoma gibbosus	0	5
Lactoria cornuta	0	3
Tetraodontidae		
Amblyrhynchotes hypselogeneion	0	3
Arothron immaculatus	3	6
Arothron stellatus	1	3
Canthigaster compressa	8	8
Canthigaster valentini	2	0
Lagocephalus sceleratus	1	1
Total number of species	51	64
Species common to both methods	32	
All species	82	

Table 2

Number of species per station according to transects and trawls, St. Vincent Bay, New Caledonia. CI = confidence interval at $\alpha = 0.05$.

	Station number									
	1	2	3	4	5	6	7	8	Average	CI
Transects	13	11	18	4	16	16	14	15	13.4	9.5–17.2
Trawl	22	31	25	18	20	38	21	27	25.3	19.3–31.2

Chi-square value for two independent samples = 7.63. Limit value = 14.07 (7 df) at $\alpha = 0.05$ (Siegel and Castellan 1988).
Station 6 was performed at night.

Table 3

Comparison of fish lengths given by transects and trawling for main species, St. Vincent Bay, New Caledonia.

	Trawl			Transect				
Species	L	n	$s\sqrt{n}$	L	n	$s\sqrt{n}$	F	t
Saurida undosquamis	22.7	108	0.07	23.3	8	1.10	**	0.50 NS
Platycephalus sp.	14.6	12	0.29	15.0	1			
Leiognathus rivulatus	8.2	130	0.07	9.2	499	0.41	-	1.30 NS
Lethrinus nematacanthus	12.2	186	0.12	14.3	244	0.08		14.9 **
Scolopsis temporalis	14.0	22	0.58	14.8	4	0.25	**	1.16 NS
Upeneus tragula	12.0	26	0.60	14.8	30	0.55	NS	3.46 **
Upeneus sp. aff. *asymetricus*	10.9	329	0.07	12.0	46	0.20		5.52 **
Pristotis jerdoni	9.1	46	0.08	8.7	490	0.04	–	4.92 **
Paramonacanthus japonicus	9.0	30	0.13	10.0	1			–
Pseudalutarius nasicornis	11.3	3	0.83	12.6	5	1.12	–	0.78 NS
Canthigaster compressa	8.3	217	0.06	8.6	38	0.20		1.62 NS

L = length in cm,
n = sample size,
$s/\sqrt{n}$ = standard error,
F = Fmax test for homogeneity of variance (Sokal and Rohlf 1981) performed if $n<30$,
t = Student test if F not significant, otherwise t' test for samples of unequal variance (Sokal and Rohlf 1981),
** = significant at $\alpha = 0.01$,
NS = not significant at $\alpha = 0.05$, dashes indicate not calculated.

Abundance and biomass

Density estimates from transects were on average 9.7 times larger than from trawls, this difference being highly significant (F test for paired comparison (Sokal and Rohlf 1981) at $\alpha = 0.01$) (Table 4). Depending on the species, the ratio between the two methods varied from 0.9 to 80 (Table 5). If one considers only the eight most common species mentioned in the previous section, then the ratio is 7.93. This would indicate a catchability of the trawl net of 0.103 for all species and 0.127 for the main species. Species for which the ratio is close to 1 (Synodontidae, *Canthigaster compressa*, *Upeneus* spp.) are difficult to detect underwater. This can be due to either their behavior (e.g., Synodontidae are usually motionless on the bottom, and at times, half buried in the sand) or to their coloration (*Canthigaster compressa* being well camouflaged among algae, and *Upeneus* spp. being able to drastically change their coloration to mimic the bottom). In addition, Table 6 indicates that these criptic species are usually found singly or in pairs.

Species with a high ratio (Apogonidae, *Leiognathus rivulatus*, *Pristotis jerdoni*) are not caught by the net for two main reasons. Either they are too small (Apogonidae, most *Pristotis jerdoni*) or they swim too high above the bottom (*Leiognathus rivulatus* were usually 0.5–3 m above the bottom) for the net to catch them. These fish are also found in small schools (21–36 fish/sighting) (Table 6). The correlation between the two methods (Table 5) is some indication of the patchiness of the distribution of these species. Thus a high correlation such as for the Synodontidae ($r = 0.75$) or *Leiognathus rivulatus* ($r = 0.92$), indicates that these

Table 4

Density estimates (fish/ha) for all species for visual transects and trawls, St. Vincent Bay, New Caledonia. CI = confidence interval ($\alpha = 0.05$).

	Station number									
	1	2	3	4	5	6	7	8	Average	CI
Transect	6020	7190	1930	8650	2610	1160	1750	4340	4200	1690–6700
Trawl	245	620	183	312	590	920	197	380	431	200–662

F test value for paired comparison = 15.1. Limit value = 5.59 (1, 7 df) at $\alpha = 0.05$.

Table 5

Comparison of density and biomass estimates from transects and trawls for main families and species, St. Vincent Bay, New Caledonia.

Family or species	Density		Biomass	
	ratio	r	ratio	r
Synodontidae	0.88	0.75*	0.80	0.93**
Apogonidae	80	0.66	13	0.78*
Lethrinus rivulatus	33	0.92**	49	0.97**
Lethrinus nematacanthus	7.4	−0.03	10	0.02
Upeneus spp.	2.3	0.63	4	0.57
Pristotis jerdoni	29	0.04	39	0.03
Canthigaster compressa	1.2	0.49	1.3	0.40
All species	9.7	−0.17	9.1	0.72*
Main species (see text)	7.9	0.23	6.4	0.34#

Ratio = density from transects/density from trawls,
r = correlation coefficient,
* significant at $\alpha < 0.05$, ** significant at $\alpha < 0.01$.
# night station (n°6) not included.

Table 6

Average distance between sightings and number of fish per sighting for main families and species, St. Vincent Bay, New Caledonia.

Family or species	Average distance between sightings (m)	Number of fish per sighting
Synodontidae	110	1
Apogonidae	260	35
Lethrinus rivulatus	120	36
Lethrinus nematacanthus	28	4
Upeneus spp.	35	1.8
Pristotis jerdoni	80	21
Canthigaster compressa	55	1.3

species are rather uniformaly distributed on the bottom. Conversely, species such as *Lethrinus nematacanthus* ($r = 0.03$) or *Pristotis jerdoni* ($r = 0.04$) have a very patchy distribution. A pratical consequence is that a larger number of stations will be needed to get a good stock assessment for the latter species than for the former.

Biomass estimates from transects are 9.1 times larger than those from the trawls (Table 7), this difference being significant (F test for paired comparison (Sokal and Rohlf 1981) at $\alpha = 0.05$). Although density estimates for all species were not correlated between trawls and transects ($r = -0.17$), biomass estimates show some correlation between the two methods, if the night station n°6 is excluded ($r = 0.72$, significant at $\alpha = 0.07$). The absence of correlation between the two methods in the density estimates may be explained by the large contribution of small fish such as Pomacentridae to transect density estimates, whereas these species escape the net. Conversely, biomass estimates are almost unaffected by these species because of their small weight. At the species level the correlations between the two methods for biomass estimates are of the same magnitude as those observed for density estimates.

Discussion

The comparison of two methods with such different concepts requires some adjustments. Trawls swept approximately 5600 m^2 and transects covered between 700 and 1000 m^2 (depending on species) for each station. The trawls did fish over the transect lines, but a perfect match would mean a trawl track with a precision of ±1 m which is untractable even in shallow water. This is, in our opinion, the main source of difference in the number of species given by each method.

Table 7

Biomass estimates (kg/ha) for transects and trawls, St. Vincent Bay, New Caledonia. CI = confidence interval at $\alpha = 0.05$.

	Station number									
	1	2	3	4	5	6	7	8	Average	CI
Transect	225	242	49	65	160	43	123	74	123	53–193
Trawl	10	19	8.3	4.9	11	34	15	6	13.5	5.0–22.0

F test value for paired comparison = 15.0. Limit value is 5.59 (1, 7 df) at $\alpha = 0.05$ (Sokal and Rohlf 1981).

Because of the low number of stations, this difference in sampled area may also be important to explain the low correlation between the two methods for density or biomass estimates of fish with a patchy distribution. Conversely, comparisons of the density or biomass for fishes with a regular distribution should not be affected.

An important result from the present survey is the magnitude of the difference between trawl and transect estimates of density. This difference, which is a factor of 9.7 for all species and a factor of 7.9 for the main species, certainly indicates that shrimp trawls poorly sample the bottom fish fauna in St. Vincent Bay. Visual transects are usually performed as strip transects, where distance of the fish to the transect line is not taken into account (Harmelin-Vivien et al. 1985). This underestimates density, especially if the width chosen is large (Burnham et al. 1980). The method chosen in the present survey is more accurate; however, it is not possible to know by how much one underestimates or overestimates the "real" density. Fish numbers (Harmelin-Vivien et al. 1985) and distances are both underestimated but play opposite roles in the density estimation. Even in the unlikely case of a large overestimate of fish density (let's suppose by 100%) by transects, the catchability of the trawl would still be 0.25 for the main species and 0.21 for all species.

Several surveys indicate that trawls may not be as efficient as usually thought. Thus Uzmann et al. (1977) found that estimates of fish density from submersibles were 8.0 times greater than density estimates from otter trawls, this ratio varying between 0.8 and 18 depending on the species. Similarly, Gray and Bell (1986) found that poisoning indicated densities 2.5 to 6.5 times greater than a beam trawl over seagrass beds. However, in some conditions trawling may be more efficient, as shown by Harden Jones et al. (1977) who used accoustical tags to estimate that 44% of the tagged flatfishes *Pleuronectes platessa* were caught by a Granton otter trawl. Uzmann et al. (1977) had found that only 7% of the flatfishes seen from a submersible were caught by the otter trawl. Serebrov (1986) used submersibles to show that the catchability of an otter trawl varied with the size of the fish, mesh size, and overall catch composition.

In the case of one or a few species, catchability of trawls may vary between 0.5 and 1.0. Such values of catchability are widely used, even in multispecies tropical fisheries, for which Pauly (1982) states that a value of 0.5 is "realistic" and Gulland (1979) even suggests that a catchability of 1.0 should apply to the eastern Indian Ocean trawl fisheries. In many of these fisheries, shrimp trawls of design similar to the one used in the present experiment are used to get a mixed catch of shrimp and fish (Grantham 1980, Poiner and Harris 1986, Lamboeuf 1987, Sainsbury 1987). Our results indicate a catchability near 0.1 (0.103 for all species and 0.127 for the main species). Such a value may need further testing; but if it proved correct, it would have important implications in the management of these tropical multispecies trawl fisheries. In particular, depending on whether one uses a catchability of 1.0 or 0.1, stock size will increase by a factor of 10. This would also affect the estimated fishing mortality (Pauly 1982) and, as a result, most of the equations used in stock management. What is more important, in our opinion, is that if one applied a catchability of 0.1 in most of these tropical trawl fisheries of the Indo-Pacific, the current models would be unable to explain the long-term decline of the catch seen in these fisheries. This could mean that trawling induces detrimental changes in fish populations which are beyond the simple removal of fish. In particular, habitat changes may be important, as noted by Poiner and Harris (1986) and Sainsbury (1987).

Another question arising from the present work is the value of the catch per unit effort (CPUE) of trawls as an indicator of population abundance. Our results show a poor correlation between abundance estimates from trawls and visual transects at the population level, but good correlations for a few selected species. Numerous studies have examined the correlation of CPUE by trawling and acoustic surveys. Most of these indicate good correlations (see Tesler (1977), Olsen et al. (1977), or Thorne (1977a) among others) but important varia-

tions may result from fish behavior (Thorne 1977b). However, most of these surveys are performed on a single pelagic or semipelagic species, and the correlation between acoustic surveys and CPUE by trawling for multispecies tropical stocks is currently poorly documented. Soetre and Paula e Silva (1979) found from comparison between demersal trawl catch and echointegration on a multispecific stock off Mozambique that the catchability of the otter trawl was 0.3. These authors state that this value is "suspiciously low for demersal species." Guillory et al. (1982) concluded from replicate sampling with otter trawls that this type of gear should be used strictly for qualitative purposes in a multispecies situation. This is in part supported by the present work, which indicates a need for alternate methods of stock assessment. Longlines show similar problems to trawling. Thus, correlation between longline CPUE and observed densities from a submersible was weak at the multispecies level (Richards and Schnute 1986, Ralston et al. 1986) but satisfactory for some selected species. Similar work involving longline CPUE and observed densities by visual transects indicated a good correlation for all species ($r = 0.88$) but considerable variations depending on species (Kulbicki 1988). Visual census either by diving or from submersible might be an alternative, but these methods also have numerous limitations. In particular, they do not allow a quick coverage of large areas and are not usable in turbid waters. If reasonably accurate density estimates are required in a multispecies tropical trawl fishery, it is likely that this can be achieved only by a combination of several independent methods.

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Abstract.—Relationships between mussel shell growth and environmental parameters were investigated in the mussel *Mytilus edulis* at an inshore location, Avila Beach, and at an offshore location, oil platform Holly (ARCO). Temporal patterns of mussel growth were similar at both locations. Mussel growth rate was related to chlorophyll *a* concentration at Holly, but not at Avila. Theoretical estimates of scope for growth (SFG) were made for mussels at each location using published physiological data. Good agreement was found, with a time lag, between estimated SFG and shell growth. The SFG analysis independently supported the conclusion that temporal changes in phytoplankton concentration limits mussel growth at Holly, but suggested that changes in the composition, rather than the concentration, of suspended particulates limits growth at Avila, as reported for mussels in estuarine environments.

Food Availability as a Limiting Factor to Mussel *Mytilus edulis* Growth in California Coastal Waters

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Temporal variability in growth rate has been extensively documented for many species of filter-feeding marine invertebrates. Growth rates frequently vary "seasonally," with most rapid growth occurring during the spring and summer months. Season is an ambiguous concept, however, which does not satisfactorily describe factors regulating temporal patterns of growth. Ultimately, environmental factors, which vary over time and with location, contribute to variation in growth rates. The growth rate of mussels *Mytilus edulis* varies in both time and space. Mussel growth rates near Santa Barbara, California, are highest from May through August (Harger 1970; Page and Hubbard 1987), but elevated rates can also occur during the winter months (Page and Hubbard 1987). Physiological and ecological evidence indicates that in many situations worldwide, food availability may be the most important single factor regulating mussel growth (Seed 1976, Widdows et al. 1979, Incze et al. 1980, Rodhouse et al. 1984). Multiple regression and correlation analysis indicated that mussel growth rate was associated with phytoplankton abundance, but not water temperature, at an offshore location in the Santa Barbara Channel (Page and Hubbard 1987).

Variation in the concentration and composition of phytoplankton and other suspended particulates which could influence mussel growth exists in the open coastal environment. For example, episodic upwelling and high primary productivity characterize the region north of Point Conception, California, relative to the Santa Barbara Channel (Owen 1980, Willason et al. 1986). Inshore areas tend to be more productive and to possess higher total seston concentrations than offshore areas, and phytoplankton concentration varies with depth (Raymont 1980). Little information is available regarding spatial relationships between phytoplankton abundance and mussel growth in inshore waters.

In this study, we used correlation analysis and the "scope for growth" concept to evaluate the potential importance of temporal and spatial variation in food availability to mussel growth. The concept of scope for growth (SFG, Warren and Davis 1967), as applied to mussels, has been reviewed by Bayne et al. (1976a) and Widdows (1985a). SFG analysis uses physiological relationships, together with environmental parameters, to estimate the potential production of soft tissue (soma and gonad) by mussels from the general energy equation, $SFG = A - (R + U)$, where SFG = energy available for growth of soft tissue, A = energy absorbed from food, R = respiratory heat loss, and U = energy lost as excreta. Radford and Bayne (cited in Bayne et al. 1976a) and Radford et al. (1981) successfully used this concept to model

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mussel growth in British waters. SFG analysis may thus prove useful in interpreting relationships between mussel growth and environmental factors in California waters.

The present study, which continued work reported in Page and Hubbard (1987), (1) compared mussel growth rates in highly productive inshore coastal waters north of Point Conception with rates measured concurrently at offshore Platform Holly (Atlantic Richfield Company), (2) evaluated the relationship between temporal and spatial variation in growth and measurements of potential food availability, and (3) used published physiological data and the "scope for growth" concept (Bayne et al. 1976a) to provide an independent assessment of the response of mussel growth to environmental conditions in California waters.

Figure 1
Locations of the Avila Beach and Platform Holly study sites.

Materials and methods

Study sites

Avila Beach (35°10′N, 120°43′W) is located approximately 84 km north of Point Conception, California (Fig. 1), in a region characterized by episodic upwelling and high primary productivity (Owen 1974, 1980; Lasker et al. 1981). The study site was located at the end of the Unocal pier which extended 0.8 km into semiprotected Avila Bay. Water depth at this location was about 12 m. *Mytilus edulis* were collected intertidally on pier pilings, since subtidal mussels were scarce due possibly to starfish predation (Landenberger 1967).

Platform Holly is a 20-year-old oil and gas production platform located in 60 m of water, about 3 km offshore of Goleta, California (34°25′N, 119°52′W; Fig. 1). Mussels colonize the support members of this platform from the intertidal zone to depths greater than 18 m, and grow rapidly, achieving 50 mm shell-length in 6–8 months (Page and Hubbard 1987).

Physical and biological parameters

We collected water samples at a depth of 2 m with a Van Doren bottle every 7–10 days at each location from October 1986 to June 1987. Temperature of samples was measured by hand-held thermometer. Estimates of potential food available to mussels were made from the concentrations of seston, particulate organic matter (POM), chlorophyll *a* (an estimate of phytoplankton biomass: Lorenzen 1970, Hunter and Laws 1981), and particulate organic carbon (POC) in replicate 500-mL water samples. All water samples were prefiltered through a 300-μm nylon mesh. Seston concentration was measured using standard methods (Widows 1985b). Percent of POM (% POM) within the seston was calculated as 100 · [POM]/[seston]. Chlorophyll *a* concentration was determined using standard fluorometric methods (Parsons et al. 1984) and a Turner Designs Fluorometer. Particulate organic carbon concentration was determined using a Perkin-Elmer CHN analyzer following the methods of Rodhouse et al. (1984).

Growth rate of *Mytilus edulis*

Twenty individually numbered mussels (~20 mm shell-length), collected intertidally (~ – 15 cm), were enclosed in a cylindrical vexar plastic cage (12 × 20 cm, 5-mm mesh) monthly at each site from November 1986 to June 1987. Using calipers, shell-lengths of caged mussels were measured to the nearest 0.1 mm initially and after 4 weeks. No growth data are available at Avila from January and February 1987, due to lack of small mussels. Cages were submerged at depth (– 2 m) either by suspension on a weighted line (Holly) or by attachment to a pole (Avila). Cages were cleaned as needed to keep fouling to a minimum.

Transplant experiments

We conducted transplant experiments in Fall 1986 to evaluate the potential influence of mussel stock on growth rate. Forty *M. edulis* were collected from Holly on 27 September 1986 and transplanted (2 cages of 20 individuals of ~30 mm shell length) to Avila on 29 September 1986. Mussels of equal size and number were collected from Avila on 29 September 1986 and transplanted to Holly on 4 October 1986. Mussels were covered with a moist cloth in transport and maintained in unfiltered seawater prior to placement in the field.

Mention of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Physiological parameters and relationships used in SFG analysis of *Mytilus edulis*. W = soft tissue dry wt. (g), L = shell length (mm), [seston] = seston concentration (mg/L), T° = water temperature (°C).

Physiological parameter	Regulatory factor(s)	Comments	Relationship	Source
1) Clearance rate (CR, L/h)	W [seston]	Independent of temperature (a, b, c). ANCOVA adjusted common slope and mean of intercepts of CR vs. W curves from (a) combined with median slope of CR vs. [seston] relationship for three size classes in (b).	$CR = 1.73 \cdot W^{0.413} - 0.006 \cdot [seston]$ if $CR < 0.1$ L/h, then $CR = 0.1$ L/h	a) Thompson 1984 b) Widdows et al. 1979 c) Widdows 1978
2) Seston filtered (SF, mg/h)	CR [seston]	Assume 100% retention efficiency.	$SF = CR \cdot [seston]$	
3a) Pseudofeces threshold (T, mg/L)	W	Shape of pseudofeces vs. food concentration curve of (d) combined with size-specific threshold values measured by (b). Technique alluded to in (e).	$T = 3.81 \cdot \log L - 1.93$	d) Foster-Smith 1975 b) Widdows et al. 1979 e) Bayne and Worrall 1980
3b) %Pseudofeces (%Ps)	T [seston]		$\%Ps = 100 - [(86.4\ e^{0.288\ T}) [seston]^{0.43 + 0.01\ T}]$	
4) Seston ingested (SI, mg/h)	SF %Ps		$SI = SF - (SF \cdot \%Ps/100)$	
5) Absorption efficiency (AE)	%POM	Model of (f).	$AE = 0.5 \cdot \log(\%POM) - 0.32$	f) Bayne et al. 1979
6) POM absorbed (A, mg/h)	SI AE		$A = (SI \cdot \%POM/100) \cdot (AE/100)$	
7) Respiratory rate (VO_2, mLO_2/h)	W T°	b value determined from average of all monthly regressions in (a). Temperature effect described by exponential curve fitted to data from (a) and (g). VO_2 considered independent of ration at [seston] >2 mg/L.	$VO_2 = a \cdot W^b$ $b = 0.782$ $a = 0.117 \cdot (10^{0.044\ T°})$	a) Thompson 1984 g) Widdows et al. 1984
8) Scope for growth (SFG, J/h)	A VO_2		$SFG = (A \cdot 23.5) - (VO_2 \cdot 20.3)$	

Growth rates of transplanted individuals were compared with that of 40 resident individuals enclosed in cages (2 cages of 20 individuals of ~30 mm shell length) and submerged at the same time.

Scope for growth

Relevant physiological parameters, regulatory factors, and relationships used in our analysis of SFG are given in Table 1. Environmental parameters required to estimate SFG (water temperature, seston concentration, and %POM) were measured in this study, while physiological relationships were derived from information in the literature.

Absorbed food was estimated from measurements of mussel size, seston concentration, %POM, and from published values for size-specific clearance rate, ingestion rate and absorption efficiency. Whenever possible, we used data on clearance and ingestion rates and

absorption efficiences obtained using "natural" POM. Clearance and ingestion rates of particulate material were assumed to be independent of water temperature, but dependent on mussel size and particle concentration (Foster-Smith 1975, Bayne et al. 1976b, Widdows 1978, Widdows et al. 1979). The fraction of filtered seston rejected as pseudofeces (% pseudofeces, Table 1) was determined from ingestion rate and the critical POM concentration (3.0 mg/L for a 20-mm mussel; Widdows et al. 1979). The percent pseudofeces represents the fraction of filtered seston rejected as pseudofeces. Absorption efficiency was estimated using the model of Bayne et al. (1979; Table 1). The caloric content of the absorbed food was assumed to be 23.5 Joules/mg dry POM (Widdows 1985b).

Metabolic expenditures were estimated given mussel size, water temperature, and published data on oxygen consumption (Thompson 1984, Widdows et al. 1984; Table 1). Published oxygen consumption measurements were converted to an energetic equivalent of 20.3 Joules/mL O_2 (Crisp 1971). Energy losses due to excretion are generally minor (as a percent of absorbed ration: 4.3–5.9%, Bayne et al. 1979; 1.7–4.3%, Widdows et al. 1980; 0.4–2.0%, Thompson 1984; 0.5–2.9%, Widdows and Shick 1985) and were ignored here. SFG (Joules/hour) was estimated as (absorbed POM, mg/hour × 23.5 J/mg) – (mL O_2/hour × 20.3 J/mL O_2).

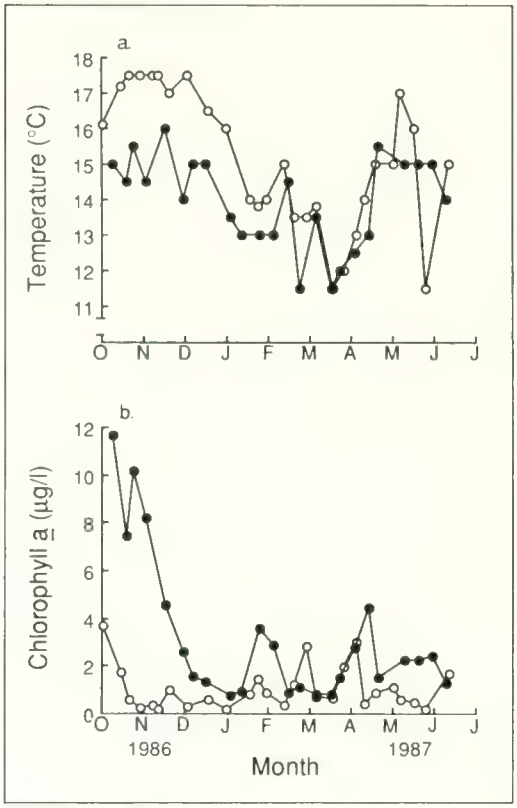

Figure 2
(a) Water temperatures and (b) chlorophyll *a* concentrations at Avila Beach (●) and Platform Holly (○).

Results

Physical and biological parameters

Surface water temperature was significantly lower at Avila than at Holly ($t = 2.46$, df = 49, $P<0.01$, Student's t-test; Fig. 2a). Water temperatures at Avila were up to 3°C cooler than at Holly from October through December 1986.

Surface chlorophyll *a* concentration was significantly higher at Avila than at Holly ($t = 3.53$, df = 49, $P<0.001$, Student's t-test; Fig. 2b). Chlorophyll *a* concentrations were as much as 20 times higher at Avila than at Holly from October through November 1986.

Seston concentration was higher at Avila than at Holly ($t = 3.88$, df = 46, $P<0.001$; Fig. 3a). The highest values at Avila (10–30 mg/L) January through February coincided with seasonal storms. Seston levels remained low at Holly, fluctuating between 1 and 5 mg/L during most of the year.

Particulate organic matter concentration was higher at Avila than at Holly ($t = 2.04$, df = 40, $P<0.05$; Fig. 3b). Particulate organic matter concentrations at Avila generally varied between 1 and 5 mg/L, but reached 10 mg/L in January 1987. Particulate organic matter concentrations at Holly ranged from <0.5 mg/L to a high value of 4 mg/L during a phytoplankton bloom in March 1987. Differences in percent POM between the two locations were most evident in January and February 1987, when percent POM was 10–35% at Avila and 40–70% at Holly (Fig. 3c).

Particulate organic carbon concentration was significantly higher at Avila than at Holly ($t = 4.88$, df = 38, $P<0.001$; Fig. 4). Values at Avila ranged from ~400 µg C/L to ~1400 µg C/L, with values exceeding 1000 µg C/L in late November 1986, and January, April, and June 1987. In contrast, POC concentrations at Holly remained below 500 µg C/L, except during March–April 1987 when values of 650–900 µg C/L were recorded. The peaks in POC concentration at Avila coincided with elevated chlorophyll *a* concentrations in November, April, and June, but not in January. The peaks in POC concentration at Holly coincided with the elevated chlorophyll *a* concentrations in March–April.

The slopes of linear least-square regression lines of POC concentration versus chlorophyll *a* concentration at Avila and Holly were significantly different from 0 ($P<0.05$, ANOVA). There was no significant difference

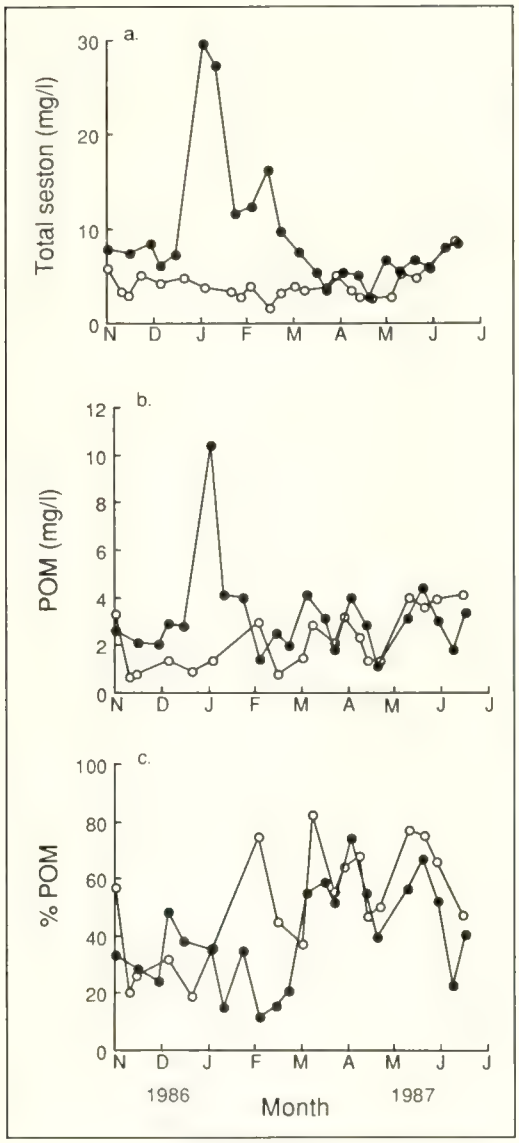

Figure 3

(a) Seston concentrations, (b) particulate organic matter (POM) concentrations, and (c) %POM at Avila Beach (●) and Platform Holly (○).

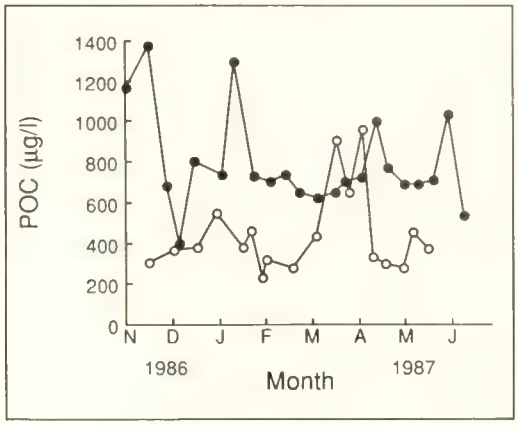

Figure 4

Particulate organic carbon (POC) concentrations at Avila Beach (●) and Platform Holly (○).

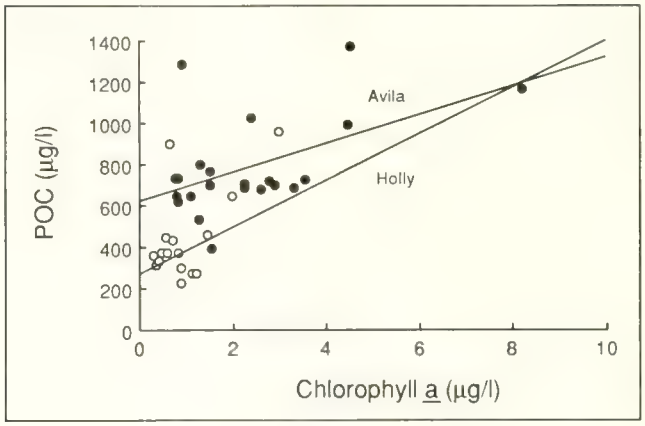

Figure 5

Linear regressions of particulate organic carbon (POC) concentration on chlorophyll *a* concentrations at Avila Beach (●) and Platform Holly (○). Avila: $y = 69.8x + 623$, $r = 0.51$; Holly: $y = 184x + 264$, $r = 0.60$.

in the slopes of these lines ($P>0.1$, ANCOVA; Fig. 5). However, a significant difference in the location of the y-intercepts ($F = 13.46$, df = 1, 34, $P<0.001$, ANCOVA) indicated that a substantially higher concentration of "background" POC existed at Avila (623 µg C/L) than at Holly (264 µg C/L).

Covariance among environmental parameters

We found weak but significant positive correlations between chlorophyll *a* concentration and both water temperature and POC concentration at Avila (Table 2).

In contrast, we found a weak negative correlation between chlorophyll *a* concentration and water temperature at Holly. Chlorophyll *a* concentration was positively correlated with both POC and POM concentration at Holly. There was no correlation between chlorophyll *a* concentration and total seston or percent POM, or between POM and POC concentration at either site (Table 2).

Growth rate

Shell growth rates for a mussel of 20 mm shell length over a period of 1 month at Avila and at Holly are given in Figure 6. Growth rate was temporally variable at both locations, with slowest growth rate December–March 1987 (5–7 mm/mo) and most rapid growth

Table 2

Correlation coefficients (r) between factors at inshore (Avila Beach) and offshore (oil platform Holly) locations, calculated from least-squares linear regression analysis. $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

Factors	Avila	Holly
Chlorophyll a : Temp	0.48*	−0.36*
Chlorophyll a : POC	0.51*	0.60**
Chlorophyll a : Seston	−0.27	0.09
Chlorophyll a : %POM	0.15	0.40
Chlorophyll a : POM	0.11	0.92***
POM : POC	0.02	0.33

Table 3

Results of transplant experiments on *Mytilus edulis* at Avila Beach and oil platform Holly. Mean values ±1 SD.

Treatment	Date	Initial length (mm)	Growth rate (mm/mo)
Avila→Holly	8 Nov. 86	29.9 ± 2.7	8.6 ± 3.1
		30.4 ± 2.9	8.0 ± 2.2
Holly	8 Nov. 86	30.0 ± 2.9	8.1 ± 2.0
		29.2 ± 3.1	7.4 ± 2.0
Holly→Avila	5 Nov. 86	33.3 ± 3.4	7.5 ± 1.9
		35.7 ± 4.2	7.4 ± 1.8
Avila	5 Nov. 86	33.6 ± 2.7	7.6 ± 1.3
		31.6 ± 3.4	7.8 ± 2.3

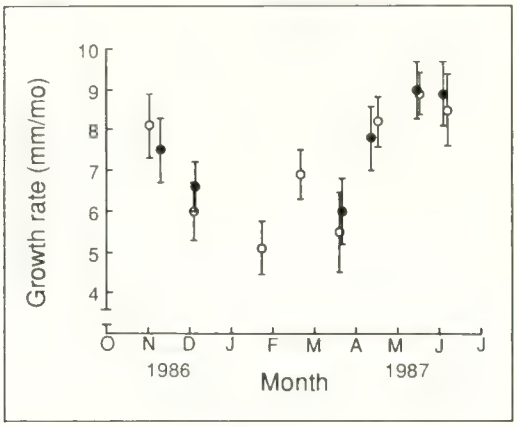

Figure 6

Length specific growth rate of a 20-mm length *Mytilus edulis* at Avila Beach (●) and Platform Holly (○). Mean values ±95% CI.

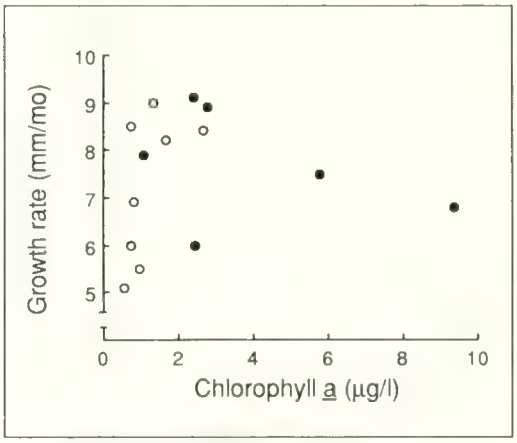

Figure 7

Relationship between *Mytilus edulis* growth rate and chlorophyll a concentration with a time lag of 3 weeks at Avila Beach (●) and Platform Holly (○).

October–November 1986 and May–July 1987 (8–9 mm/mo). There was no effect of mussel stock on growth rate ($F = 0.901$, $P>0.1$, 1-way ANOVA; Table 3). Mortality of caged mussels was <5.0%.

Relationship between growth rate and chlorophyll *a* concentration

We calculated correlation coefficients relating the growth rate of *M. edulis* to chlorophyll a concentration and water temperature for grouped Avila and Holly data integrated over the 4-week period of mussel exposure and at time lags of 0–4 weeks. There was no correlation between growth rate and chlorophyll a concentration ($P>0.05$, $n = 14$). However, growth rate correlated with chlorophyll a concentration with a time lag of 3 weeks, if the fall and winter values from Avila (when seston concentrations exceeded 5 mg/L) were excluded ($r = 0.67$, $P<0.05$, $n = 11$; Fig. 7). There was no correlation between growth rate and water temperature ($P>0.05$).

Scope for growth

A summary of our theoretical scope-for-growth calculations, averaged by month, is given in Table 4. Our analysis indicates that, overall, the estimated amount of seston filtered from suspension by mussels was higher at Avila than at Holly (4.00 vs. 1.91 mg/h, $t = 4.03$, df = 46, $P<0.001$). However, mussels at Avila had a significantly higher estimated percent pseudofeces production (48.6% vs. 13.7%, $t = 6.34$, df = 46, $P<0.001$) than mussels at Holly. Thus despite the higher seston concentrations at Avila, the actual amount of estimated POM assimilated by mussels at each locality should have been similar (0.43 mg/h at Holly vs. 0.36 mg/h at Avila, $P>0.01$).

Table 4

Summary of scope-for-growth calculations for a 20-mm shell length (0.05 g) *Mytilus edulis* averaged by month. POM = particulate organic matter.

Month	Clearance rate (L/h)	Seston filtered (mg/h)	Pseudofeces threshold (mg/L)	% pseudofeces	Seston ingested (mg/h)	Absorption efficiency (%)	POM absorbed (mg/h)	VO (mL O_2/h)
Avila Beach								
Nov.	0.45	3.55	3.0	50.62	1.76	42.40	0.23	0.06
Dec.	0.46	3.33	3.0	48.15	1.74	45.38	0.32	0.05
Jan.	0.36	8.03	3.0	74.71	2.26	39.04	0.27	0.04
Feb.	0.42	5.70	3.0	64.59	2.06	27.32	0.31	0.04
Mar.	0.47	3.48	3.0	28.87	2.32	54.94	0.70	0.04
Apr.	0.47	2.22	3.0	23.98	1.72	54.72	0.48	0.04
May	0.46	2.32	3.0	43.21	1.34	54.64	0.43	0.05
June	0.45	3.30	3.0	51.57	1.59	45.88	0.29	0.05
Oil platform Holly								
Nov.	0.48	2.02	3.0	18.58	1.54	42.49	0.24	0.07
Dec.	0.48	1.06	3.0	28.28	1.53	37.29	0.15	0.07
Jan.	0.48	1.58	3.0	0.00	1.58	48.29	0.31	0.05
Feb.	0.48	1.40	3.0	0.00	1.40	55.01	0.48	0.05
Mar.	0.48	1.92	3.0	8.44	1.72	55.90	0.58	0.04
Apr.	0.48	1.42	3.0	0.00	1.42	54.59	0.44	0.05
May	0.48	2.20	3.0	27.12	1.52	60.19	0.65	0.05
June	0.45	3.91	3.0	55.11	1.76	51.65	0.43	0.05

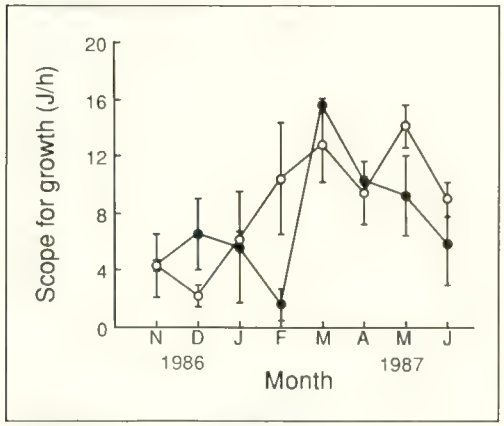

Figure 8

Estimates of monthly scope-for-growth of a 0.05-g dry weight (~20 mm shell length) *Mytilus edulis* at Avila Beach (●) and Platform Holly (○). Mean values ±1 SE.

Table 5

Results of two-way ANOVA evaluating the influence of month and location of estimated scope for growth of *Mytilus edulis*. ***$P<0.001$.

Source	Sum of square	df	Mean square	F ratio
Location	16.09	1	16.09	0.83
Month	557.95	7	79.71	4.11***
Month · Location	190.31	7	27.19	1.40
Error	640.51	33	19.41	

Figure 8 shows the monthly SFG of a 0.05 g dry weight *M. edulis* (~20 mm shell length) at Holly and at Avila, calculated using the seston concentration and percent POM data from these localities and the equations in Table 1. There was a significant effect of month, but not location, on scope for growth (2-way ANOVA, Table 5). An *a posteriori* test for significant differences among months revealed that the low SFG values of November–February differed significantly from the higher SFG values of March–June ($F = 4.11$, df = 1, 33, $P<0.001$).

To evaluate the relationship between shell growth rate and theoretical SFG, we calculated linear correlation coefficients between growth rate (Fig. 6) and scope for growth for the combined Avila and Holly data at time lags of 0–4 weeks. Growth was not correlated with SFG at a time lag of 0 weeks ($r = 0.56$, $P>0.05$). However, growth rate correlated with SFG at time lags of 1–4 weeks with strongest correlations at time lags of 2 and 3 weeks ($r = 0.70$ and 0.75, $P<0.05$, $n = 10$; Fig. 9).

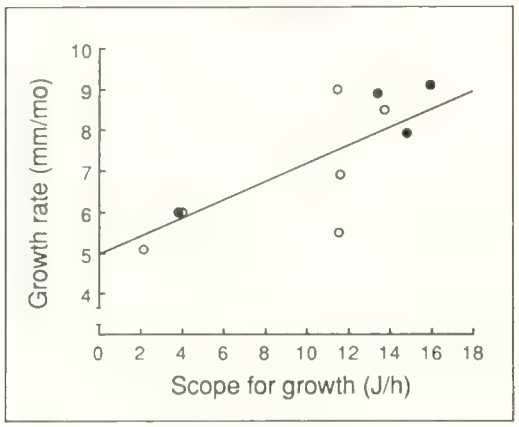

Figure 9

Linear regression of *Mytilus edulis* shell growth rate on scope for growth for combined data from Avila Beach (●) and Platform Holly (○) with a time lag of 3 weeks. $y = 0.22x + 4.96$, $r = 0.75$.

Discussion

Spatial variation in phytoplankton biomass may affect the growth and nutritional condition of filter-feeding species along the California coast (larval fish *Engraulis mordax*, Lasker and Smith 1977, O'Connell 1980; copepod *Calanus pacificus*, Willason et al. 1986; anomuran crab *Emerita analoga*, Dugan and Wenner 1985). We found that mussel growth increased with chlorophyll *a* concentration, except during the fall and winter months at Avila. The low growth rates at Avila during fall and winter, despite chlorophyll *a* concentrations exceeding 4 μg/L, may reflect a leveling-off or decline in particle ingestion rates associated with high seston concentrations (Foster-Smith 1975, Widdows et al. 1979).

Temporal patterns of growth were similar for mussels at Avila and Holly (Fig. 6). These data suggested that ingestion rate was not appreciably higher for mussels at Avila, despite the higher POC concentrations there (generally >600 μg/L). In addition, both the high background POC concentration (623 μg/L, Fig. 5) and the lack of correlation between chlorophyll *a* and POM concentrations at Avila indicated the presence of a high concentration of nonphytoplankton particulates (e.g., bacteria, microzooplankton, detritus) which may not support rapid mussel growth. *Mytilus edulis* has shown poor growth when supplied only with nonphytoplankton food sources in laboratory experiments (Winter 1974, Williams 1981).

The lack of a correlation between growth rate and water temperature for grouped data from both locations is consistent with the view that water temperature is not an important factor influencing mussel growth in California waters (Page and Hubbard 1987).

The lack of a stock or genotypic effect on mussel growth rate in our transplant experiments was not surprising, as the distance between the study sites was only about 120 km. *Mytilus edulis* has a planktonic larval stage of about 3 weeks, and typical current velocities of 0.5 km/hour (Chambers Group 1986) would permit larvae to drift as much as 250 km. *Mytilus edulis* also has the potential to delay metamorphosis and to exist as a pediveliger in the plankton for several days (Bayne 1964), facilitating genetic exchange between spatially separated populations. The transplant experiments also indicated that postsettlement selection (Koehn and Hilbish 1987), which might result in differences in growth rate between locations, was not an important factor in this study.

Our field growth-rate data generally conform to predictions from the theoretical SFG analysis. This analysis suggested that mussels at Avila and Holly absorbed similar amounts of POM and had similar SFG because seston concentrations were high at Avila (>4 mg/L) and mussels at this location had a higher rate of pseudofeces production and lower absorption efficiency than mussels at Holly. Shell growth rate correlated with theoretical SFG after incorporation of a time lag. SFG is a measure of the energy instantaneously available for the growth of soft tissue and shell. In small mussels, shell growth rate is correlated with soft tissue growth (Nielsen 1985). The time lag likely reflects the time required for metabolic conversion of absorbed energy and nutrients into the shell.

The relationships between potential food availability and mussel growth at Avila and Holly agree with general predictions developed primarily from physiological studies of *M. edulis* in British estuarine environments where the energy available for growth was regulated by the food quality, reflected by the percent POM, rather than by quantity of the seston when seston concentrations exceeded 4–5 mg/L (Bayne and Widdows 1978, Widdows et al. 1979). The growth rate of mussels in California coastal waters, with seston concentrations comparable to those at Avila, is thus likely limited by the quality rather than the quantity of the seston.

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Abstract.– Significant changes in the biomass of sandlance *Ammodytes* spp. and in the abundance of the copepod *Calanus finmarchicus* in the southern Gulf of Maine co-occurred with a shift in the occurrence and abundance of four species of baleen whales in the region. During the years 1982–88 the abundance of sandlance was negatively correlated to the abundance of *C. finmarchicus* ($r_s = -0.883$, $P<0.05$). Peak years of abundance for *C. finmarchicus* during 1982–88 in the study area were the lowest years of abundance for sandlance. The abundance of *C. finmarchicus* and sandlance was at a regional maximum during 1986 and 1988, respectively.

The abundance of humpback and fin whales were marginally correlated to each other ($r_s = 0.3338$, $P< 0.08$). The abundance of humpbacks was negatively correlated with right whales ($r_s = -0.7753$, $P<0.001$) and sei whales ($r_s = -0.5507$, $P<0.01$). The patterns of occurrence for right and sei whales were significantly related to each other ($r_s = 0.6842$, $P< 0.001$). Right and sei whales were common in the region only during 1986, when copepod abundance reached a regional maximum and sandlance abundance a regional minimum. These patterns of whale occurrence reflect known prey preferences, and are therefore expected between the pisciverous humpback and fin whales and the highly planktiverous right and sei whales.

We hypothesize that the spatial distribution and abundance of baleen whales in the Gulf of Maine can be characterized as a series of ecological responses to human-induced changes in the abundance of planktiverous finfish.

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Recent Fluctuations in the Abundance of Baleen Whales in the Southern Gulf of Maine in Relation to Changes in Selected Prey

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During the mid-1970s, a dramatic increase in the abundance of sandlance *Ammodytes* spp.* precipitated a significant change in the abundance and composition of the ichthyofauna in the shelf waters of the northeastern United States (Smith et al. 1978, 1980; Morse 1982). The population explosion of sandlance coincided with a 50% reduction in total finfish biomass in the same region between 1968 and 1975 (Clark and Brown 1977). This decrease was primarily due to the commercial depletion of stocks of herring *Clupea harengus* and mackerel *Scomber scombrus* (Anthony and Waring 1980, Grosslein et al. 1980). A concurrent increase in sandlance abundance following the depletion of North Sea herring and mackerel stocks led Sherman et al. (1981) to suggest that sandlance had taken over ecological niches previously occupied by these species in many areas of the Northwest Atlantic.

Since the mid-1970s sandlance have become increasingly important in the Gulf of Maine as prey for commercial fish (Bowman et al. 1984), seabirds (Powers and Backus 1987), pinnipeds (Payne and Selzer 1989), and baleen whales (Overholtz and Nicolas 1979, Hain et al. 1982, Payne et al. 1986). Sandlance were the only confirmed prey of the humpback whale *Megaptera novaeangliae* between 1975 and 1979 (Hain et al. 1982, Mayo 1982) and the only prey significantly correlated with the distribution of humpbacks in the Gulf of Maine between 1978 and 1982 (Payne et al. 1986). Also, fin whales *Balaenoptera physalus*, sympatric with humpbacks in this region, have frequently been observed exploiting sandlance (Overholtz and Nicolas 1979).

Two other species of large baleen whales, the northern right whale *Eubalaena glacialis* and the sei whale *Balaenoptera borealis*, also occur in

* Two species of this genus, *A. americanus* and *A. dubius*, occur in the shelf waters of the northeastern United States (Richards et al. 1963, Reay 1970, Richards and Kendall 1973, Meyer et al. 1979, Richards 1982).

the Gulf of Maine (CeTAP 1982, Watkins and Schevill 1982, Kraus 1985, Schevill et al. 1986, Weinrich et al. 1986, Hamilton and Mayo 1990). Both of these species have been characterized principally as "skim feeders" (Nemoto 1959, Kawamura 1974, Nemoto and Kawamura 1977) which subsist primarily on dense swarms of calanoid copepods, notably *Calanus finmarchicus* in the North Atlantic (Mitchell 1975a, 1975b; Jonsgard and Darling 1977; Mitchell and Chapman 1977; Winn et al. 1986; Wishner et al. 1988; Mayo and Marx 1990), in preference to schooling fish (Watkins and Schevill 1979).

This similarity in prey preference led Mitchell (1975a) to hypothesize that competition between these two whale species might have adversely affected the recovery of the right whale in the western North Atlantic. However, sandlance are also known to play an important trophic role as a major predator of copepods, especially *C. finmarchicus* (Monteleone and Peterson 1986, Meyer et al. 1979). Given their abundance and prey selectivity towards copepods, Kenney et al. (1986) proposed that sandlance represented a more significant competitor to right whales for copepodite prey than sei whales (as suggested by Mitchell 1975a).

The existence of some degree of intra- and interspecific competition between right/sei whales and sandlance (ecologically similar species) for a common prey is generally accepted, but is difficult to demonstrate. An overlap in preferred prey is at best a qualitative phenomenon, and offers only "soft corroboration" (from Strong et al. 1984) as evidence for competition between these species. Another approach (used by Smith 1968, 1970; Eck and Wells 1987), which we have adopted for the purpose of this study, is to look for a demonstrable shift in the ecological balance between competing species, or the complete replacement of one competing species by another. In this paper we examine the ecological relationships between sandlance and two of its major predators, the humpback and fin whale; between sandlance and its major prey, the copepod *Calanus finmarchicus*; and between sandlance and two potential competitors for *C. finmarchicus* in this region, the right and sei whale.

Methods

Study area

In this paper we have focused on Stellwagen Bank (Fig. 1), a glacial deposit of sand and gravel in the southwest Gulf of Maine that is associated with high levels of biological productivity and a rapidly developing commercial whalewatching industry. The margins of the bank are defined by the 40-m isobath with depths as low as 18 m. Since the early 1980s whalewatching vessels have provided intensive survey coverage of cetaceans in the area from June through September of each year.

Collection and treatment of data

Fisheries data Data on the abundance of sandlance used here were collected on Stellwagen Bank and immediately adjacent waters by National Marine Fisheries Service, Northeast Fisheries Center (NMFS/NEFC) biologists and technicians during standardized NMFS/NEFC spring bottom-trawl surveys. The NMFS/NEFC survey area has been spatially stratified into approximate ecological units based principally on depth (see Grosslein 1969). Stellwagen Bank is a principal bathymetric feature in the Gulf of Maine–NMFS/NEFC stratum #26. The number of sandlance caught per tow in stratum #26 (for each spring survey) was transformed into logarithmic values, and the mean number of sandlance (transformed data) was considered representative of Stellwagen Bank and used in all further analyses, a procedure which follows that described in Payne et al. (1986).

The *Calanus finmarchicus* data were also collected by NMFS/NEFC personnel. A transect across the Gulf of Maine has been sampled with the Hardy Continuous Plankton Recorder (CPR) since 1961 (Jossi and Smith 1990). Since the early 1980s a desired sampling frequency of one transect per month has been generally achieved. Data used in this study came from the 10-nautical-mile section of the transect centered on Stellwagen Bank. Water passing through the CPR is filtered with bolting silk having mean aperture dimensions of $225 \times 234\ \mu$. All large zooplankton (≥ 2 mm) in the sample are identified and enumerated. Counts of smaller (≤ 2 mm) zooplankton are made from an aliquot ($\sim 1/45$) of the sample. Counts were converted to number of organisms per 100 m^3, and then transformed to log base 10 for subsequent calculations. Further details of this procedure are given in Colebrook (1975) and in Jossi and Smith (1990). All reference to copepod data and abundance used in this study exclusively concern *C. finmarchicus*.

The abundance of sandlance (expressed as the mean of the log-transformed number of sandlance per tow/year) and of the copepod *C. finmarchicus* (log-transformed number of individuals/100 m^3/year) were compared by first ranking the data by year, 1982–88 ($N = 7$), then calculating Spearman's coefficient of rank correlation (r_s) (Zar 1984). The data are therefore compared on an ordinal, rather than on an absolute, scale; this is because of the magnitude of the difference in the scale of the data that were brought together for this study.

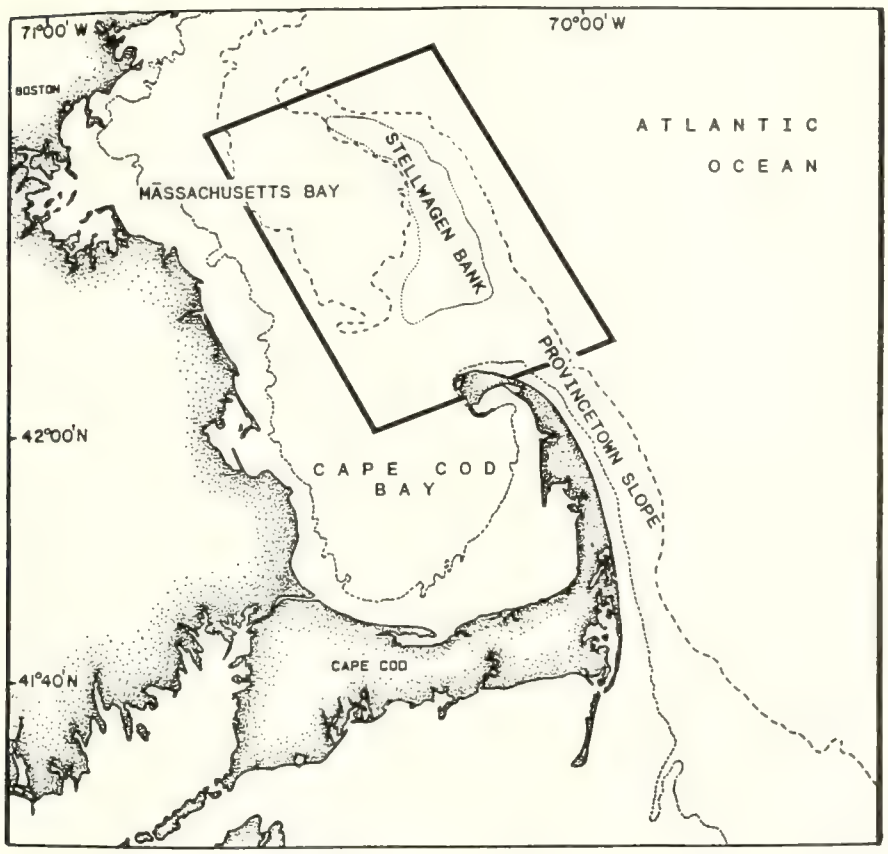

Figure 1
Baleen whale study area in southern Gulf of Maine (outlined) and geographical regions referred to throughout the text.

Whale sighting data Data for this study on the occurrence and distribution of humpback, fin, right, and sei whales were collected by naturalists working aboard commercial whalewatching vessels during the study period 1982–88. Data recorded from these vessels for all cetacean sightings include species, group size, time, location (using LORAN-C), behavior, and the photographically confirmed identity of individual animals. Vessels ran 4-hour cruises to the Stellwagen Bank and Massachusetts Bay areas from two ports: Provincetown and Plymouth, Massachusetts. The cruise track of the whalewatching vessels was decided by the captain based upon the greatest number of whale sightings recorded on the previous trip or day; consequently, sampling was neither random nor systematic. Nonetheless, the intensity of the coverage resulted in extremely comprehensive surveys of the region during most of the study period. The information collected aboard these vessels in this region represents one of the most detailed databases available anywhere on a multispecies group of whales.

Data used in this study were taken from the first cruise of each day from each of the two ports and considered a reliable index of relative abundance of whales in the area. The total number of whales observed during each morning whalewatching trip from each port was summed by species and month, June–September (the period when coverage from whalewatching vessels was effectively continuous). These totals were then divided by the number of trips each month (each trip was considered a unit of effort), resulting in an index of whale abundance, expressed as number of whales/effort/month for each species between 1982 and 1988. While there are undoubtedly biases associated with the collection of these data, the intensity of coverage is such that this index can be used to accurately monitor relative changes in the local abundance and distribution of whales.

Using these sighting data, the temporal co-occurrence between the four whale species within the study area was tested by ranking the mean number of whales/effort/month (by species), then calculating Spearman's coefficient of rank correlation (r_s) (Zar 1984) between species for all paired data, 1982–88 ($N = 28$ for each possible pairing).

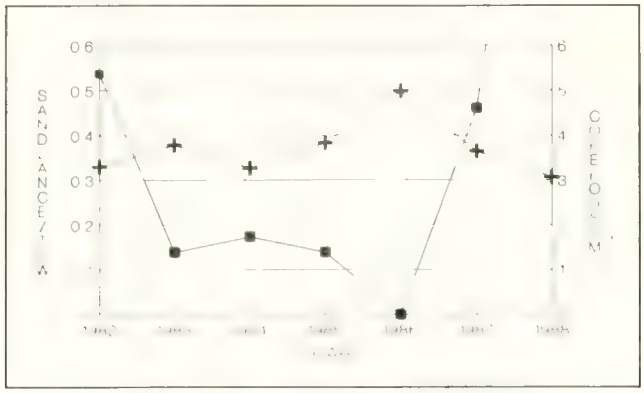

Figure 2
Stratified mean number of sandlance (■) per tow (log transformation) on left, and the number of copepods *Calanus finmarchicus* (+) per m^3 (log transformation) on right. Note: the scale for sandlance is different from that of copepods.

Results

Changes in abundance of sandlance and copepods

The mean number of sandlance per tow (log transformation) collected during spring bottom-trawl surveys ranged between years (Fig. 2) from a minimum 0.000 (in 1986) to a maximum 4.066 per tow (in 1988). Two trends were apparent. The data show a decline in catches from 1982 to the zero value of 1986. Catches increased in 1987, peaking in 1988 to 4.066 sandlance per tow (log value). The number of sandlance caught in 1988 was a regional abundance maximum for spring surveys, 1968–88 (from information presented in Nelson and Ross 1989).

The log-transformed values of *C. finmarchicus*/m^3 of water collected in the CPR ranged from 3.270 (in 1984) to 4.988 (in 1986), and generally increased on Stellwagen Bank between 1982 and 1986 (Fig. 2). The increase was most apparent between 1984 and 1986. The number of *C. finmarchicus* collected in 1986 was one order of magnitude greater than that collected during any other year of the study. Following 1986 the number of *C. finmarchicus* declined rapidly to 3.640 (log value) in 1987, then to 3.070 (log value) in 1988 (Fig. 2).

The abundance of sandlance on Stellwagen Bank was inversely related to the abundance of *C. finmarchicus* ($r_s = -0.883$, $P<0.05$, $N = 7$). The three years when the spring tow values for sandlance were the lowest (1983, 1985, and 1986) were the three peak years for *C. finmarchicus* (Fig. 2). Conversely, the number of *C. finmarchicus* recorded on Stellwagen Bank during 1988 was one of the lowest throughout the study period. This is the year when the sandlance reached its maximum peak of abundance.

Changes in whale abundance

Humpback and fin whales showed a similar trend in abundance ($r_s = 0.3338$, $P<0.074$, Table 2), although the variation in the observed number of humpbacks between years was much more pronounced than for fin whales. The number of humpbacks/year increased from 3.59 whales/effort in 1982 to 9.00 whales/effort in 1985 (Table 1, Fig. 3). During 1986 humpback abundance declined to the minimum value recorded during the study period of 0.23 whales/effort. A small increase in 1987 was followed by a much larger increase in 1988 to 6.98 whales/effort (Fig. 3).

Less dramatic fluctuations between years were evident in the number of fin whales from 1982 to 1988. The abundance of fin whales declined from the maximum value of 3.71 whales/effort in 1984 to the low values of 1.9 and 1.4 whales/effort recorded in 1986 and 1987, respectively (Fig. 3). Although the numbers of fin whales/effort were lower in 1986–87 than in previous years, they did not change by more than an order of magnitude, as did other whale species. The number of fin whales increased to 3.61 whales/effort in 1988.

The strongest positive correlation occurred between right and sei whales ($r_s = 0.6842$, $P<0.0001$, Table 2). The right whale is a rare but regularly occurring species whose temporal occurrence in the study area has been generally restricted to the months of late-winter through early-spring (Winn et al. 1986, Brown and Winn 1989, Hamilton and Mayo 1990). This pattern was generally repeated in all years of the study period except 1986. Excluding 1986, there were only 12 right whale sightings from 1982 to 1988, and during most years there were no sightings (Table 1). However, in 1986, 174 right whale sightings (0.95 whales/effort) were recorded, and right whales were observed virtually every day throughout the summer (Hamilton and Mayo 1990).

Sightings of sei whales on Stellwagen Bank, and in Cape Cod Bay, are very rare in any season (CeTAP 1982, Mayo et al. 1988). We did not observe sei whales in the study area between 1982 and 1985 (Table 1). However, their numbers increased significantly in 1986 (when they were commonly observed) to 0.26 whales/effort (Table 1, Fig. 3). The occurrence of sei whales in 1986 was followed by an equally dramatic decline during 1987 (2 sightings, 0.01 sei whales/effort) and 1988 (no sightings). Between 1982 and 1988, the sei whale and right whale were abundant only during 1986 (Fig. 3), when the abundance of *C. finmarchicus* also reached a recorded regional maximum (Wishner et al. 1988).

Table 1

Total number of whales counted, number of surveys (effort), and number of whales (by species) per survey in southern Gulf of Maine (in parentheses) for each month and year of the study, 1982–88.

Year	Month	No. of surveys	No. of whales (per survey) Humpback	Fin	Right	Sei
1982	June	27	90(3.33)	45(1.67)	0.00	0.00
	July	31	228(7.35)	33(1.06)	0.00	0.00
	Aug.	31	54(1.74)	227(7.32)	0.00	0.00
	Sept.	27	45(1.67)	63(2.33)	4(0.15)	0.00
	Total	116	417(3.59)	368(3.17)	4(0.03)	0.00
1983	June	46	229(4.98)	60(1.30)	0.00	0.00
	July	43	266(6.19)	192(4.47)	0.00	0.00
	Aug.	36	169(4.69)	172(4.78)	0.00	0.00
	Sept.	28	96(3.43)	37(1.32)	0.00	0.00
	Total	153	760(4.97)	461(3.01)	0.00	0.00
1984	June	43	317(7.37)	26(0.60)	0.00	0.00
	July	45	382(8.49)	224(4.98)	0.00	0.00
	Aug.	47	261(5.55)	232(4.94)	0.00	0.00
	Sept.	33	133(4.03)	141(4.27)	0.00	0.00
	Total	168	1093(6.51)	623(3.71)	0.00	0.00
1985	June	40	411(10.30)	143(3.58)	0.00	0.00
	July	53	400(7.55)	122(2.30)	0.00	0.00
	Aug.	46	654(14.21)	154(3.35)	0.00	0.00
	Sept.	31	63(2.03)	24(0.78)	0.00	0.00
	Total	170	1528(8.99)	443(2.61)	0.00	0.00
1986	June	44	16(0.36)	62(1.41)	2(0.05)	0.00
	July	54	20(0.37)	136(2.52)	6(0.11)	2(0.04)
	Aug.	51	4(0.08)	93(1.82)	44(0.86)	19(0.37)
	Sept.	34	2(0.05)	102(3.00)	122(3.58)	26(0.76)
	Total	183	42(0.23)	344(1.88)	174(0.95)	47(0.26)
1987	June	55	30(0.55)	56(1.02)	2(0.04)	0.00
	July	61	36(0.59)	48(0.79)	1(0.02)	2(0.03)
	Aug.	55	76(1.38)	150(2.73)	0.00	0.00
	Sept.	47	12(0.25)	52(1.10)	5(0.11)	0.00
	Total	218	154(0.71)	306(1.40)	8(0.04)	2(0.01)
1988	June	55	199(3.62)	253(4.60)	0.00	0.00
	July	62	535(8.63)	263(4.24)	0.00	0.00
	Aug.	62	455(7.34)	160(2.58)	0.00	0.00
	Sept.	52	424(8.15)	159(3.06)	0.00	0.00
	Total	231	1613(6.98)	835(3.61)	0.00	0.00

Table 2

Spearman Rank Correlation Coefficients (r_s) (upper number) and statistical level of significant difference (P) (lower number) between the abundance (whales/effort) of four baleen whale species on Stellwagen Bank, 1982–88. N = 28 for all paired tests.

	Humpback	Fin	Right	Sei
Humpback	1.0000	0.3338	−0.7753	−0.5507
	0.0000	0.0740	0.0001	0.0019
Fin		1.0000	−0.3250	−0.1461
		0.0000	0.0643	0.4248
Right			1.0000	0.6842
			0.0000	0.0001
Sei				1.0000
				0.0000

Several significant negative relationships also occurred between whale species (Table 2), most noticeably between humpbacks and right whales (r_s = −0.7753, P<0.0001), humpbacks and sei whales (r_s = −0.5507, P<0.0019), and fin whales and right whales (r_s = −0.3250, P<0.0643). This supports an intuitive interpretation of the data shown in Figure 3, notably the obvious phenomenon of low humpback and fin whale abundance in 1986, the only year right and sei whales were observed in significant numbers.

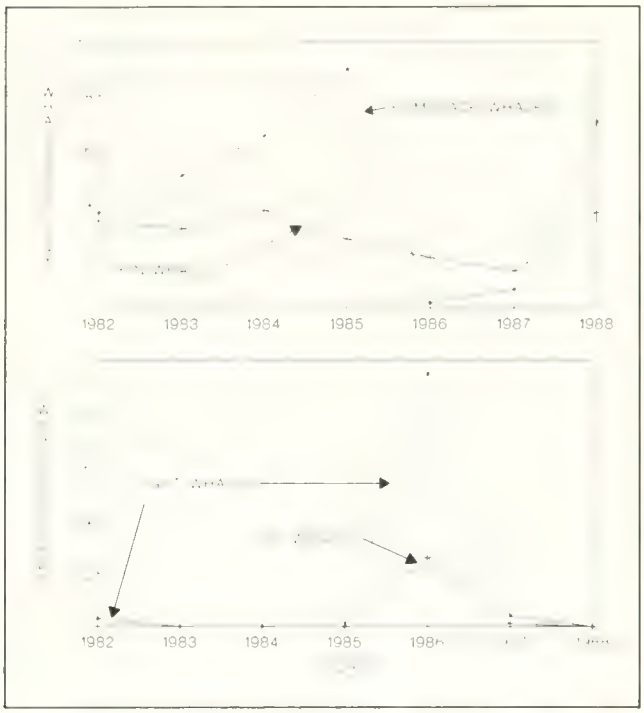

Figure 3
Average number of baleen whales per unit effort for each year of the study by species. Note: the scale for humpback and fin whales (upper) is different from that of right and sei whales (lower).

Discussion

The data presented here strongly suggest that major changes which occurred in the abundance and distribution of humpback, fin, right, and sei whales in the Stellwagen Bank area, 1982–88, were not independent of each other. During 1986 a dramatic decline in the abundance of humpback and fin whales also co-occurred with the unusual occurrence of right and sei whales during the summer of the same year. During 1987 and 1988 the abundance of baleen whales returned to a pattern similar to that observed in years prior to 1986 (right and sei whales absent, humpback and fin whales abundant). Concurrent with changes in whale abundance, an increase in copepod abundance on Stellwagen Bank in 1986 correlated with a significant decline in local sandlance abundance.

These correlations likely reflect both the similarities and dissimilarities in prey preferences of individual whale species, and the predator-prey relationship between sandlance and copepods. Given the documented preference of both right and sei whales for copepods (Nemoto 1959, Mitchell 1975a, Nemoto and Kawamura 1977, Watkins and Schevill 1979), a strong positive correlation between the two species should be expected. A similar correspondence exists between humpback and fin whales, both of which show an apparent preference for schooling fish in this region (Watkins and Schevill 1979, Mayo et al. 1988). Conversely, the strong negative correlations reported here would be expected between the planktiverous right and sei whales and the pisciverous humpback and fin whales.

Competition between whale species

These results, in support of previous studies (Kenney et al. 1981, Payne et al. 1986), suggest that the recent distribution of humpback whales in the Gulf of Maine has been dependent on the spatial distribution of sandlance in that region. These results follow a trend which began in the mid-1970s and, when taken with the results of previous studies (Overholtz and Nicolas 1979, CeTAP 1982, Hain et al. 1982, Mayo 1982, Mayo et al. 1988), indicate that sandlance has been the most important prey item of humpback whales in the Gulf of Maine since at least 1976.

It is also of interest that, while fin whales also closely followed the abundance patterns of sandlance, the overall changes in fin whale abundance fluctuated much less than those shown for the humpback whale. Although both whale species prey on a variety of taxa (Jonsgaard 1966) and have been characterized as generalists in their dietary preferences (Mitchell 1975a), behavioral differences between the two species may result in the ability of fin whales to exploit prey other than sandlance in the study area.

Watkins and Schevill (1979) noted clear differences between the feeding behavior of humpback and fin whales when exploiting the same prey (schooling fish); fin whales lunge horizontally and humpbacks vertically. Humpbacks are also known to produce "bubble clouds or nets" to potentially concentrate prey (Jurasz and Jurasz 1979, Hain et al. 1982, Hays et al. 1985), a feeding method not observed for fin whales. It has also been suggested that the streamlined form and greater speed of fin whales allow them to exploit more widely separated patches of prey than humpbacks (Brodie 1975, Whitehead and Carlson 1988). Thus fin whales may be more independent of local fluctuations in prey availability, explaining why they were located in the study area in 1986, after humpbacks had abandoned it.

Evidence clearly exists to support the belief that competition exists between right and sei whales (Mitchell 1975a, Kawamura 1978). However, Kenney et al. (1986) suggested that competition between right and sei whales in the shelf waters of the northeastern United States is unlikely given their present allopatric distributions (excluding 1986). Perhaps the more important ecological question concerns the reason for the present apparent allopatry. As detailed below, we

believe that this recent distributional change has resulted from differing degrees of interspecific competition between each of the two whale species and sandlance, moreso than from any competition between the whales themselves.

Competition between sandlance and planktiverous whale species

Historically, and in recent times, right whales have been recorded in the Stellwagen Bank region in late winter and early spring (Allen 1908, Allen 1916, Watkins and Schevill 1982, Schevill et al. 1986, Hamilton and Mayo 1990). The species has been virtually absent from the area in summer, when the population's distribution is centered in the Bay of Fundy and on the Scotian Shelf (Kraus et al. 1982, 1986; Mitchell et al. 1986; Winn et al. 1986; Stone et al. 1988; Murison and Gaskin 1989). Therefore, the prolonged residency by a group of right whales in the Stellwagen region throughout summer 1986 may represent the most significant departure from their usual seasonal pattern of occurrence recorded this century.

Is the annual movement of right whales out of the southern Gulf of Maine and into the Bay of Fundy and Scotian shelf areas in early summer related to increased activity and competition from planktiverous fish for calanoid copepods? The question of why right whales generally undertake this northward migration has yet to be resolved. The occurrence of right whales in the Stellwagen Bank area in the summer of 1986 implies that, if certain conditions are met, the normal northward movement is not inevitable for at least part of the population. The occurrence of planktiverous fish (either sandlance, herring or mackerel)—and consequently of increased competition through predation on, or disruption of, copepod patches in spring—may be a major factor in directing the seasonal movement of right whales out of the area to seek more acceptable patches elsewhere in the Gulf of Maine.

Not only are the size and density of copepod patches important to the feeding energetics of right whales, but also the relative proportions of adult copepods within each patch (Wishner et al. 1988). Wishner et al. (1988) described a copepod surface patch (with associated skim-feeding right whales) which contained a regional maximum of copepodite IVs and Vs, the older, energetically richest, developmental stages of copepods (Comita et al. 1966). Although the feeding ecology of right whales is likely more complex than previously thought (Mayo and Marx 1990), these dense aggregations of older, caloric-rich copepods seem to be the required characteristics for energetically successful foraging by right whales (Kenney et al. 1986, Wishner et al. 1988).

The principal diet of sandlance >21 mm is also the larger, older developmental stages of *C. finmarchicus* (Norcross et al. 1961, Scott 1973, Monteleone and Peterson 1986). If the superabundant sandlance are selecting the caloric-rich stages of the copepod population, then there may be insufficient prey available in the remaining developmental stages (independent of abundance) to provide right whales with the required energy densities (as described by Kenney et al. 1986) to meet the metabolic and reproductive demands of the right whale population. Therefore, during those years when sandlance (or ecologically similar planktiverous fish species) are abundant, intraspecific competition may be so intense that right whales may only be achieving basal metabolic needs in the southern Gulf of Maine, precipitating the northward movement of right whales immediately following the period of increased sandlance abundance and activity.

The occurrence of consistent numbers of sei whales in 1986 followed many years in which the species had not been recorded from the study area during any season (Mayo et al. 1988). Jonsgaard and Darling (1977) describe "invasion years" where unusually large numbers of sei whales occur in an area. These years are generally followed by an equally sharp decrease in the number of whales in the same area. Albeit simple, an "invasion year" in response to increased prey abundance accurately describes the occurrence of sei whales on Stellwagen Bank during 1986.

While sei whales seem to prefer planktonic prey (Watkins and Schevill 1979), they have the ability to forage on fish (Nemoto 1959, Nemoto and Kawamura 1977). Despite this, available distributional evidence suggests that sei whales have not exploited the abundant sandlance in the Gulf of Maine to a significant extent. Scant data suggest that sei whales in this region instead subsist primarily on euphausiids and copepods which occur in the waters south of Georges Bank (Kenney and Winn 1987). By remaining on the shelf edge and exploiting a wider range of planktonic (and possibly fish) prey, they may be able to minimize the effect of competition from sandlance for copepods, separating them from the more stenophagic right whales.

Since the early 1950s sandlance populations have fluctuated on remarkably few occasions. Monteleone et al. (1987) described relatively high sandlance densities during 1965–66 (following the depletion of herring and mackerel stocks) and 1978–79 (following the larval sandlance explosion in 1975), and exceptionally low densities of sandlance in 1971–74. Meyer et al. (1979) also reported that adult sandlance were not reported on Stellwagen Bank between 1967–76 and that the mean sandlance catch/10 m^2 in spring 1977 was nine times greater than in spring 1974. Therefore, the two recorded time intervals when sei whales and

right whales were most abundant in the study area (April 1970, reported by Watkins and Schevill 1982; and during 1986) were during periods of documented low adult sandlance densities and observed copepod maxima. The March 1975 observations by Watkins and Schevill (1979) of a sei and right whales feeding together in Cape Cod Bay were also made in the interval between the reduction of planktiverous herring and mackerel stocks and the subsequent population explosion of adult sandlance. These observations further support the theory that planktiverous fish abundance has negatively impacted the occurrence of planktiverous whale species in the region.

In this paper, we have examined species interactions between sandlance (as prey and competitor), *C. finmarchicus* (as prey), and the abundance of four species of baleen whales in the southern Gulf of Maine. The interpretation of these interactions, although largely inductive, provide useful management insights into the relationships between planktiverous finfish and the cetacean community. This interpretation also presents an interesting multispecies-management dilemma regarding finfish and cetacean populations in this region, as well as potential conflicts between single-species recovery plans and two ecologically different groups of endangered whales, pisciverous and planktiverous.

The present abundance of sandlance in the Gulf of Maine followed a long-term depletion of other planktiverous fish species through overfishing (Grosslein et al. 1980). Although it is impossible to reconstruct the extent of competition between finfish (herring and mackerel stocks) and planktiverous whales prior to the mid-1960s, the similarities in prey preference and trophic relationships between mackerel, herring and sandlance (Bowman et al. 1984) certainly suggest that competition between herring-mackerel stocks and planktiverous whales could have existed. We hypothesize that the abundance and distribution of planktiverous fishes have played a significant, perhaps critical, role in structuring (as prey and competitor) baleen whale populations in the Gulf of Maine.

The present, concentrated distribution of humpbacks in the Gulf of Maine is directly related to the distribution and increased abundance of sandlance in that region. Alternatively, the recovery of the stenophagic right whale (historically and at present) may indeed be inhibited in large regions of the northwest Atlantic by competition for its prey by herring, mackerel, and sandlance. Despite decades of protection Schevill et al. (1986) suggested that the [abundance of the] right whale population [now] which passes Cape Cod is "at worst slightly smaller than it was in the 17th century". The abundance and distribution (and continued recovery) of right whales, in contrast to humpback and fin whales, may be contingent upon anomalous disruptions in the occurrence of abundant, ecologically equivalent finfish stocks, which at present are largely human-induced.

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Abstract.– Coastal cutthroat trout and steelhead, which are sympatric over much of their range along the Pacific coast of North America, have different behaviors in both freshwater and the ocean. Juveniles of both species were caught in purse seines off the Oregon and Washington coasts during the early summer, sometimes over 46 km offshore. However, both species were absent from catches in September. Cutthroat apparently returned to freshwater, whereas steelhead migrated far offshore during late summer. Ocean growth rates of smolts of both trouts were similar, about 1 mm per day; but since cutthroat spend little time in the ocean, they are small at maturity. This is possibly an adaptation related to spawning short distances from the ocean or in small tributaries upstream of the spawning and rearing habitats of other anadromous salmonids. Cutthroat trout fed primarily on fishes, but steelhead had a more varied diet in coastal waters, consuming fishes but also euphausiids and other crustaceans.

Distribution and Biology of Juvenile Cutthroat Trout *Oncorhynchus clarki clarki* and Steelhead *O. mykiss* in Coastal Waters off Oregon and Washington

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Two species of anadromous trout are native to the Pacific coast drainages of North America: *Oncorhynchus c. clarki* (formerly *Salmo c. clarki*), the coastal cutthroat trout, and *O. mykiss* (formerly *Salmo gairdneri* and *S. mykiss*), the steelhead and Kamchatkan trout (Smith and Stearley 1989). The coastal cutthroat trout ranges from northern California to southeastern Alaska. The native range of the steelhead trout was from the Alaska Peninsula to Baja but now is found only as far south as central California (Carl et al. 1959, MacCrimmon 1971, Scott and Crossman 1973).

Because these two trout species are sympatric over much of their range (Scott and Crossman 1973, Behnke 1979) behavioral and ecological differences are of special interest. Coastal cutthroat select small tributaries for spawning, rarely over 160 km inland, whereas steelhead prefer larger streams and sometimes migrate long distances from the ocean. Coastal cutthroat usually spawn slightly earlier in the year (January–March) than steelhead (February–April) (Needham and Gard 1959, Withler 1966, Hartman and Gill 1968, Scott and Crossman 1973, Johnston 1982). These differences in location and time of spawning apparently help maintain reproductive isolation between these species (Needham and Gard 1959, Trotter 1989).

Anadromous wild stocks of both species of trout usually spend 2–4 years in freshwater before smoltification and downstream migration to the ocean, while hatchery stocks commonly migrate to the sea after one year in freshwater. Downstream migrations of smolts of both species usually peak in April or May (Chapman 1958, Lowry 1965, Withler 1966, Armstrong 1971, Giger 1972, Sutherland 1973, Okazaki 1984, Dawley et al. 1985, Loch and Miller 1988) or in late May or early June in Alaska (Armstrong 1971).

Our knowledge of the marine life history and ecology of steelhead and cutthroat trout is meager. In this

paper we describe the distribution and movements, age and size distribution, sex ratios, and food habits of juveniles of these species in coastal waters off Oregon and Washington as determined by purse seine catches, discuss the differences between these species, and speculate on their adaptive significance.

Methods

Cutthroat trout and steelhead were captured in purse seines in the northeastern Pacific Ocean during May–September, 1980–85. Data from 1981–85, the years of most extensive sampling, are the basis for most of this paper (see Pearcy and Fisher 1988, for sampling details). A total of 992 quantitative seine sets were made with a 457–495 m seine with 32-mm (stretch measure) mesh that fished to depths of 20–65 m. Sets were made along east-west transects off Oregon and Washington (43°00′N to 48°21′N) at 9.3 km (5 n.mi.) intervals out to about 50 km offshore (Fig. 1). During July 1984, we sampled over a broader area, from northern California (40°32′N) to Vancouver Island (50°26′N).

Trout were identified, measured (fork length, FL), examined for marks, and either released or preserved by freezing at sea. A total of 15 cutthroat and 8 steelhead were tagged with Floy tags and released. In the laboratory ashore, the preserved fish were measured, weighed, scales were removed, stomachs excised, and gonads were examined.

Scales from cutthroat trout and steelhead were collected from an area 1–3 scale rows above the lateral line along the diagonal scale row from the insertion of the dorsal fin (Clutter and Whitesel 1956). Scales were mounted on gummed cards from which acetate impressions were made. The impressions were magnified 88×. All measurements were made in the anterior half of the scale along an axis 20° ventrad to the long axis. Ages of smolts at ocean entrance were estimated by counting the bands of narrowly spaced or broken circuli (interpreted as winter annuli) in the freshwater growth zone of the scale. These freshwater ages are estimates because occasionally "checks," which were difficult to interpret, occurred in the freshwater growth zone and few scales from fish of known freshwater age were available for comparison. The abrupt change from relatively narrowly to widely spaced circuli indicated the transition from freshwater to ocean growth. Subsequent zones of narrowly spaced circuli or resorption on cutthroat trout scales were interpreted as evidence of slow growth from reduced feeding or spawning in freshwater [see Sumner (1962, 1972) and Loch and Miller (1988) for scale interpretations and photographs]. All juvenile steelhead collected were in their first summer in the ocean and had not yet spawned.

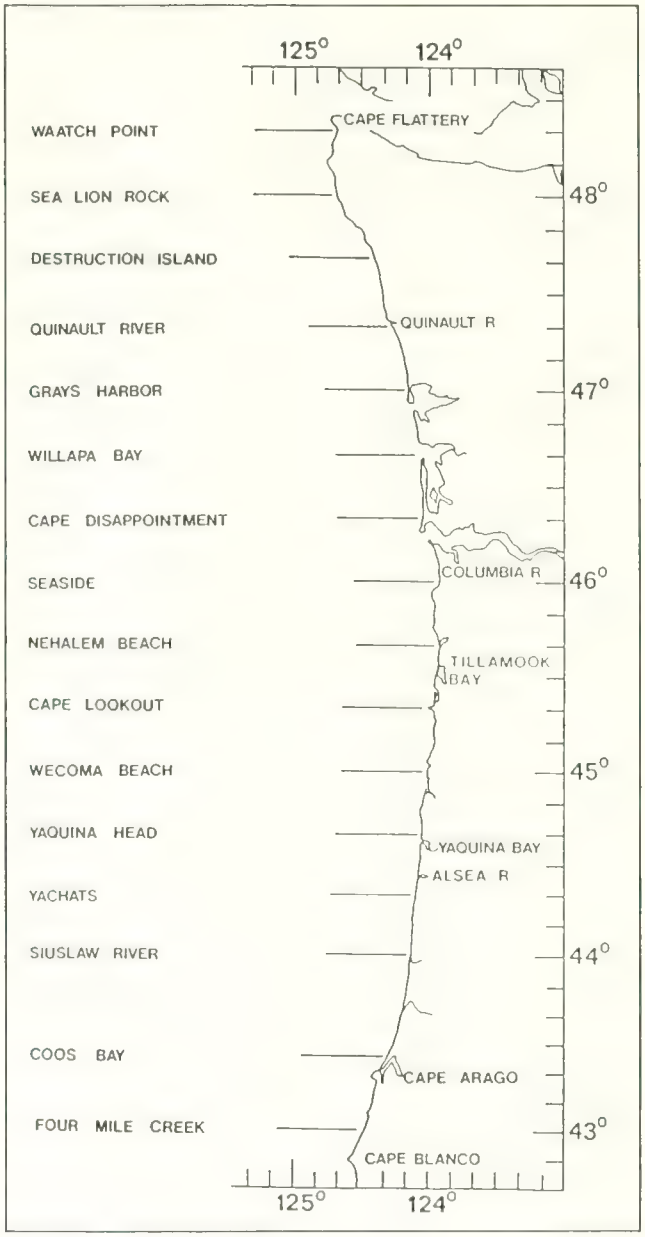

Figure 1
Location of purse seine transect lines off Oregon and Washington.

Size at ocean entrance of cutthroat and steelhead trout caught during their first ocean summer was back-calculated using the method of Lee as described in Carlander (1981):

$$Li = a + ((Lc - a)/Sc) \cdot Si,$$

where Li = FL (mm) at time of ocean entry
Lc = FL (mm) when captured
Sc = total scale radius (mm at 88×)
Si = scale radius at time of ocean entry

a = the y intercept of the regression of FL on scale radius.

The y intercepts (a) for each species were determined from the geometric mean regressions of FL and scale radius (Ricker 1973) from juvenile fish caught in the ocean (cutthroat repeat spawners excluded):

Steelhead

$$FL(mm) = 51.1 + 1.69 \cdot Sc \text{ (mm at } 88\times), \; n = 84, \; r = 0.73, \text{ FL range} = 143\text{–}288 \text{ mm}$$

Cutthroat

$$FL(mm) = 62.1 + 2.26 \cdot Sc \text{ (mm at } 88\times), \; n = 101, \; r = 0.70, \text{ FL range} = 175\text{–}369 \text{ mm.}$$

Sc-FL relationships for both species appeared linear over the length ranges of fish examined. Back-calculation of size at ocean entrance using natural logarithm transformations of FL and Sc (Bartlett et al. 1984, Hooten et al. 1987) produced only very small differences ($\bar{x}$ 1 mm) in back-calculated lengths compared with untransformed data.

We estimated ocean growth for each steelhead and cutthroat trout by subtracting the back-calculated FL at time of ocean entry from the FL at time of capture in the ocean. Growth rates in the ocean of individual fish were estimated from ocean growth back-calculated from scales divided by estimated days in the ocean. To arrive at estimates of time spent in the ocean we used dates of ocean entry corresponding to the beginning, middle, and end of the period of smolt migration into the ocean, yielding several estimates of growth rate for each fish. Seaward migration of cutthroat trout smolts through the Columbia River and coastal Oregon estuaries generally takes place from late March or early April through May (Giger 1972, Loch and Miller 1988, Dawley et al. 1985), with maximum numbers of smolts occurring in the Alsea estuary in the second week of May (Giger 1972). By the end of May very few cutthroat trout smolts were found in the Alsea estuary (Giger 1972). Almost all steelhead smolts passed river kilometer 75 in the Columbia River estuary between 15 April and 15 June, with half the migration completed by the third week in May (Dawley et al. 1985). We used ocean entry dates of 1 April, 1 May, 10 May, and 31 May to estimate growth rates of cutthroat trout, and 15 April, 1 May, and 17 May to estimate growth rates of steelhead. Although ocean entry of steelhead smolts probably continued until about the middle of June, almost all of our catch of steelhead occurred before 15 June.

We also estimated average growth rate of cutthroat trout from the slope of the regression of back-calculated ocean growth on julian date, a method in which no assumptions are made about a precise time of ocean entry. This method was possible because captures of cutthroat in the ocean extended well past the period of smolt entry into the ocean.

Stomach contents were preserved in 10% buffered formalin, transferred to 70% ethanol prior to examination, and weighed to the nearest mg after removal of excess moisture. Contents were examined with a dissecting microscope and were identified to the lowest possible taxon. Total lengths of intact fish prey were measured to the nearest mm. Percent frequency of occurrence in non-empty stomachs (F), percent of the total number of prey organisms (N), and percent of the total wet weight of prey organisms (W) were determined and combined in the Index of Relative Importance (IRI = F(N + W)). Dietary overlaps were calculated from a Percent Similarity Index (= Σ minimum percent weights of taxa in common between two groups of fish). A total of 67 cutthroat (<300 mm in length) and 98 steelhead stomachs were examined from the collections made in 1980–85. The food habits of 48 larger (>300 mm) cutthroat collected during this study were presented by Brodeur et al. (1987a).

Results

Abundance

A total of 163 cutthroat and 134 juvenile steelhead trout were collected during our cruises in 1981–85. These species combined comprised about 3% of our catches of juvenile salmonids (Pearcy and Fisher In press). Cutthroat and steelhead trout were captured from May through August, and occurred in 0–30% and 2–24%, respectively, of the seine sets during these months (Table 1).

Frequencies of occurrence and catches per set of steelhead were generally highest in May and June and were much lower in July and August (Table 1). Steelhead were absent in September of all years. Abundances of cutthroat trout in 1981, the year of most regular sampling, were highest in July and about the same in May, June, and August. Like steelhead, cutthroat trout were absent in September of all years (Table 1).

Distributional trends

In most years, average catches of cutthroat trout were higher in the region off southern Washington and northern Oregon, near the mouth of the Columbia River (Zone B), than off northern Washington (Zone A) or Oregon south of the Columbia River (Zone C) (Table 2). No obvious latitudinal trends were noted

Table 1

Percent frequency of occurrence (FO), mean catch per set (CPS), and number (n) of juvenile cutthroat and steelhead trout caught in purse seine collections, 1981–85, off Oregon and Washington. (S indicates total number of purse seine sets by month.) No steelhead or cutthroat trout were collected in September 1982, 1983, or 1984 (n = 38, 51, and 63 sets, respectively). NS indicates no sets were taken during those months.

	May S = 208			June S = 327			July S = 130			August S = 66		
	FO	CPS	n	FO	CPS	n	FO	CPS	n	FO	CPS	n
Cutthroat												
1981	13	0.29	18	9	0.19	13	30	0.61	41	12	0.21	14
1982	5	0.13	8	14	0.16	9	NS	NS	NS	NS	NS	NS
1983	9	0.13	7	7	0.14	8	NS	NS	NS	NS	NS	NS
1984	NS	NS	NS	6	0.11	7	3	0.05	3	NS	NS	NS
1985	25	0.46	13*	19	0.28	22	NS	NS	NS	NS	NS	NS
Steelhead												
1981	22	0.51	32	15	0.37	25	7	0.07	5	2	0.02	1
1982	24	0.52	32	4	0.04	2	NS	NS	NS	NS	NS	NS
1983	7	0.07	4	3	0.03	2	NS	NS	NS	NS	NS	NS
1984	NS	NS	NS	8	0.12	8	6	0.08	5	NS	NS	NS
1985	18	0.29	8*	6	0.13	10	NS	NS	NS	NS	NS	NS

*Late May and early June sampling off the Columbia R. mouth.

Table 2

Average catch per set of cutthroat/steelhead trout in purse seine sets off Oregon and Washington, during May, June, and July combined, 1981–85 (number of sets in parentheses). NS = no samples.

Zone	1981	1982	1983	1984	1985
A Cape Flattery to Grays Harbor, WA	NS NS	0.04/0.46 (26)	0.05/0.08 (37)	0/0.15 (33)	0/0.10 (20)
B Willapa Bay, WA to Nehalem, OR	0.58/0.54 (111)	0.16/0.31 (45)	0.21/0.03 (33)	0.32/0.16 (25)	0.50/0.15 (54)
C Tillamook Bay to Cape Blanco, OR	0.09/0.02 (86)	0.19/0.17 (47)	0.14/0.47 (43)	0.02/0 (48)	0.23/0.23 (34)
D Extended cruise					
Swiftsure Bank to Winter Harbor, B.C.				0/0 (15)	
Cape Blanco, OR to False Cape, CA				0/0.5 (8)	

for steelhead. Steelhead were captured as far south as northern California during the extended cruise of July 1984.

The highest average catches of both cutthroat and steelhead trout occurred 37.2–46.3 km offshore (Table 3). Low catches of both species were found in the zone closest to shore (<9.3 km). Catches of cutthroat were high 37.2-46.3 km offshore only in May and June 1985, when juvenile coho salmon were also found far offshore (Fisher and Pearcy 1985). In other years highest catches of cutthroat were 9.4–27.8 km offshore, inshore of maximal steelhead catches. The zone of highest average catches for all years was characterized by a mean sea surface temperature of 13.4°C (standard deviation, SD, 1.4), mean surface salinity of 28.6‰ (SD 4.3) and secchi depth of 5.4 m (SD 2.2). The low surface salinities in areas where steelhead and cutthroat trout were abundant indicate the influence of freshwater, often the Columbia River plume. Detailed spatial information on catches is given by Pearcy and Fisher (In press) by cruise.

Table 3

Mean catch per set of cutthroat and steelhead trout and standard deviation at varying distances from the Oregon/Washington coast, 1981–85, giving equal weight to each cruise (15 cruises sampled inshore of 46 km, except 9 cruises at 46.4–55.6 km, and 2 cruises at >55.6 km).

Distance offshore:	km / n.mi.	<9.3 <5	9.4–18.5 5–10	18.6–27.8 10–15	27.9–37.1 15–20	37.2–46.3 20–25	46.4–55.6 25–30	>55.6
Cutthroat	$\bar{x}$	0.09	0.25	0.17	0.15	0.33	0.03	0.10
	SD	0.09	0.26	0.25	0.28	0.61	0.10	0.14
Steelhead	$\bar{x}$	0.03	0.09	0.16	0.23	0.52	0.19	0
	SD	0.06	0.09	0.23	0.36	0.81	0.38	–

Table 4

Release and recapture data for tagged cutthroat and steelhead trout off Oregon and Washington.

Release			Capture		Days between release and recovery	Distance N/S of release (km)	Tagged FL (mm)	Recovered FL (mm)
Date	Location	Code	Date	Location				
Cutthroat								
12 June 85	Yaquina Head	Floy	25 July 85	Siuslaw R.	43	72 S	294	–
18 June 85	Cape Disappoint.	Floy	Fall 85	Umpqua R.	–	290 S	295	–
Steelhead								
27 March 22 May 81	Quinault R., WA	050758	9 June 81	Leadbetter Pt., WA	18–74	85 S		172
4 May 81	Clearwater R., ID	102252	21 May 81	Warrenton, OR	17	9 S		206
14 May 82	Quinault R., WA	051043	31 May 82	Cape Lookout, OR	17	269 S		185
4 May 84	Clearwater R., ID	051335	10 June 84	Cape Disappoint.	37	9 N		194
22 June 83	Cape Disappoint.	Floy	9 Sept. 83	Jones Beach, Col. R.	79	11 S	445	495

Tag recoveries

Two of the cutthroat trout tagged with Floy tags on our cruises in 1985 were recovered by fishermen, one 43 days after release 72 km south of the tagging location and the other 290 km south of the tagging location (Table 4). We also caught four hatchery coded-wire tagged steelhead smolts in the ocean 17–74 days after hatchery release. The two released in the Clearwater River, Idaho, were captured close to the mouth of the Columbia River where they entered the ocean. Two fish released in the Quinault River, Washington, were recovered 85 km and 269 km south of where they entered the ocean. Movements to the south by these two steelhead and the cutthroat trout may have been related to advection of surface waters during the upwelling season (Pearcy and Fisher 1988).

Of the eight maturing steelhead tagged, one (445 mm FL) tagged off Cape Disappointment near the mouth of the Columbia River was recaptured 79 days following its release at 495 mm FL in the Columbia River. Its growth rate between release and recapture was 0.63 mm/day.

Age, lengths, and sex ratios

Of the 110 cutthroat trout with readable scales, 32%, 45%, 19%, and 3% migrated to sea for the first time after one, two, three, and four winters in freshwater (ages 1., 2., 3., and 4.)*, respectively (Table 5). This is a younger age distribution than found by Giger (1972) for wild cutthroat trout from coastal Oregon river systems, but similar to that found by Loch and Miller (1988) in the ocean off the Columbia River mouth. Most of the age 1. cutthroat we caught probably originated from hatcheries (Loch and Miller 1988), including hatcheries on the Columbia River.

Most cutthroat were immature or maturing fish on their first ocean migration (age .0). Only eight fish had scales that showed evidence of reduced growth (a

* Age designation follows that recommended by Koo (1962), and used by others (Godfrey et al. 1975, Hartt and Dell 1986), where the numbers before and after the decimal point refer to winters spent in freshwater prior to first migration to the ocean and winters spent in the ocean, respectively. Ages 1., 2., 3., etc. designate the freshwater age of a fish without reference to its ocean age.

Table 5

Freshwater age* and number of repeat spawners, as determined from scale analysis, and lengths of cutthroat and steelhead trout caught in ocean purse seines off Oregon and Washington.

	Cutthroat					Steelhead			
			Fork length (mm)					Fork length (mm)	
Month	Freshwater age	No. of fish	$\bar{x}$	SD	No. repeat spawners	Freshwater age	No. of fish	$\bar{x}$	SD
May	1.	10	267	46.1	2	1.	35	216	32.5
	2.	12	258	38.7	1	2.	19	185	17.2
	3.	7	279	27.9	1	3.	7	204	17.9
	4.	1	284	—	0	4.	0	—	—
June	1.	13	280	57.4	2	1.	17	209	28.7
	2.	16	282	48.0	1	2.	7	225	36.2
	3.	8	314	16.1	0	3.	2	257	31.8
	4.	2	271	8.5	0	4.	0		
July	1.	10	284	40.9	0	1.	1	260	—
	2.	16	299	34.8	0	2.	1	246	—
	3.	5	336	27.2	1	3.	0		
	4.	0	—	—	0	4.	0		
August	1.	3	321	10.1	0	1.	0		
	2.	6	316	17.9	0	2.	0		
	3.	1	314	—	0	3.	0		
	4.	0	—	—	0	4.	0		
Total		110			8		89		

*See text footnote, p. 701, for explanation of age designation.

winter annulus or spawning check) after initial ocean entrance ("repeat spawners," Table 5). Six of these had apparently made one previous migration from the ocean to freshwater, and two had made two previous trips to freshwater. All of these fish measured 335–380 mm FL except for one 279 mm FL fish. Half of the repeat spawners had first entered the ocean after one winter in freshwater (age 1.). Seven of the eight prior spawners were collected in May or June, probably soon after reentering the ocean.

All juvenile steelhead caught in the ocean were in their first ocean summer (age .0). Of the 89 steelhead that had readable scales, 60%, 30%, and 10% were ages 1.0, 2.0 and 3.0, respectively (Table 5). Ten of 11 steelhead caught with clipped adipose fins, probably denoting hatchery origin, were age 1.0. Since most wild steelhead enter the ocean after two or three winters in freshwater and most hatchery steelhead after only one winter (Chapman 1958, Withler 1966, Pauley et al. 1986), the majority of fish we caught were probably of hatchery origin.

Length ranges were broad for both cutthroat trout and steelhead during each month (1981–85 combined, Fig. 2). This may have resulted from variable size and age of smolts entering the ocean (Loch 1982, Dawley et al. 1982, Bottom et al. 1984, Ward and Slaney 1988) or variable growth rates. During downstream migration, the length ranges of individual hatchery groups of steelhead smolts can be very broad. For example, Dawley et al. (1986) found length ranges of 150–270 mm FL and 110–240 mm FL for two groups sampled in the upper Columbia River estuary.

Back-calculated length at time of ocean entry of cutthroat trout averaged 241 mm FL, but was quite variable (SD 38 mm, $n = 101$, repeat spawners excluded). Age 3.0 fish tended to be larger at time of first ocean entry than younger fish or age 4.0 fish (average back-calculated FL at ocean entry = 231, 239, 264, and 244 mm FL for age 1.0, 2.0, 3.0, and 4.0 fish, respectively). Our average back-calculated lengths at ocean entry for cutthroat trout caught at sea were larger than those back-calculated by Giger (1972) for wild cutthroat of the same age from the Alsea, Nestucca, and Siuslaw Rivers (239 vs. 210 and 264 vs. 239 mm FL for age 2.0 and 3.0 fish, respectively). However, the mean length at ocean entry estimated by Giger for all freshwater age groups and for all three river systems combined (233 mm FL) by Giger was fairly close to our average (241 mm FL).

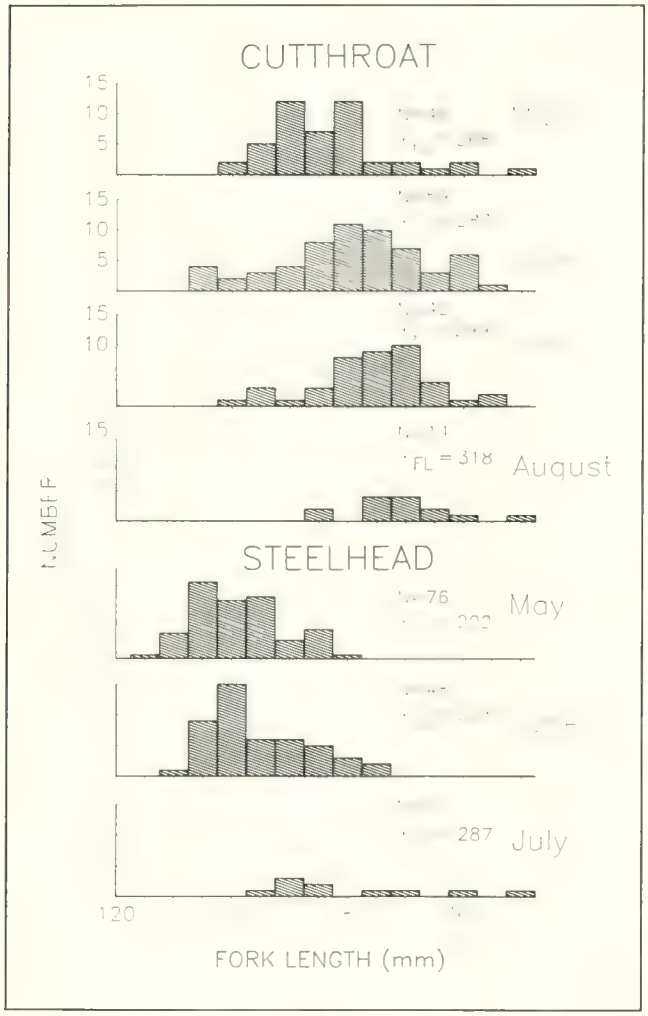

Figure 2
Size-frequency distributions of cutthroat and steelhead trout, by month, 1981–85 combined.

Mean back-calculated FL at time of ocean entry for steelhead was 199 mm (197 mm and 200 mm for fish caught in May and June, respectively) and was quite variable (SD 29 mm, $n = 84$). These estimated lengths at time of ocean entry were similar to the mean lengths of steelhead smolts caught during downstream migration in the Columbia River (~200 mm, Dawley et al. 1985, their figs. 4–10), and similar to those estimated by Narver (1969, 1974) for steelhead smolts in two British Columbia river systems (182 and 190 mm FL), but were larger than mean lengths of all ages of wild smolts from two Washington streams (156 and 165 m FL; Loch et al. 1988).

The mean lengths of both species increased during the summer. This suggests either growth in length during this time period or higher availability of larger fish later in the summer (Loch 1982, Dawley et al. 1982). Mean lengths of cutthroat trout caught in the ocean in July and August (299 and 318 mm FL, respectively) were similar to mean lengths of age 2. and 3. cutthroat trout (305 and 323 mm FL, respectively) caught in coastal Oregon estuaries from July through September on their initial spawning migrations (Giger 1972).

More male than female cutthroat were captured, but fewer male then female steelhead were caught. However, the respective sex ratios of 1.3:1 and 0.7:1 were not statistically different from 1:1 ($p > 0.1$, chi-square test). None of the cutthroat trout examined had enlarged testes or ovaries (>1% of body weight), which is expected since cutthroat spawn in the winter-spring period.

Ocean growth

Of cutthroat trout caught in the ocean in May, June, July, and August, 65, 83, 90, and 100%, respectively, showed an ocean growth pattern on their scales. Mean estimated ocean growth rates of cutthroat trout (including fish with and without ocean growth) were 0.47, 0.78, 1.03, and 2.60 mm/day, assuming an ocean entry date of 1 April, 1 May, 10 May, and 31 May, respectively. Since the median date of ocean entry of cutthroat trout smolts is sometime in early May (Giger 1972, Loch and Miller 1988, Dawley et al. 1985), growth rate estimates using 1 May or 10 May as an ocean entry date (0.78 and 1.03 mm/day) are probably closest to the true average growth rate of cutthroat trout in the ocean. Ocean growth rates based on the slope of the geometric mean regression (Ricker 1973) of back-calculated ocean growth and julian date was 1.22 mm/day ($n = 101$, $r = 0.67$), fairly close to the mean growth rates of individual fish assuming early May ocean entry dates.

Almost all juvenile steelhead with readable scales were caught in May and June. Only 30% and 50%, respectively, of the steelhead caught in these two months showed signs of ocean growth on their scales. This suggests that the steelhead caught in May and June were, on average, in the coastal ocean for less time than the cutthroat trout caught in the same months, either because of later ocean entry or rapid migration of steelhead out of coastal waters. Back-calculated ocean growth rates of juvenile steelhead (including fish with and without ocean growth) were 0.21, 0.32, and 1.06 mm/day for assumed ocean entry dates of 15 April, 1 May, and 17 May, respectively. Downstream migration of steelhead smolts in the Columbia River estuary was half completed around the third week in May (Dawley et al. 1985). Consequently, the ocean entry date of 17 May probably gives the best estimate of average growth rate in the ocean (1.06 mm/day). This growth rate was similar to the average

growth rate for cutthroat trout using an early May date of ocean entry. The lack of steelhead caught late in the summer precluded estimating mean growth rate from change in back-calculated ocean growth with time.

Food habits

Cutthroat trout Fishes were by far the dominant prey of juvenile cutthroat trout in terms of frequency, number, and weight. Hexagrammids, scorpaenids, northern anchovy *Engraulis mordax*, and the brown Irish lord *Hemilepidotus spinosus* were the dominant fish taxa identified (Appendix Table 1). One unidentified Pacific salmon, *Oncorhynchus* sp. [81 mm total length (TL)], was found in the stomach of a 221-mm cutthroat trout collected 11.4 km off the mouth of the Columbia River in July 1981. Fishes made up more than 75% of the biomass consumed during all years, but they decreased in importance in the diet as the summer progressed, so that by late summer several other prey taxa such as euphausiids, hyperiid amphipods, and decapod larvae were important. Prey fishes found in cutthroat stomachs averaged 52.5 mm TL (SD 21.8) and ranged from 21 to 101 mm. No significant relation ($n = 46$, $r = 0.30$, $p = 0.16$) was found between the lengths of cutthroat trout and their fish prey.

Steelhead The diet of juvenile steelhead trout was more diverse than that of cutthroat trout. Both arthropods and fishes were important prey items. Prey of steelhead trout ranged from small barnacle larvae and copepods to larger juvenile fishes and squids. Euphausiids, mainly *Thysanoessa spinifera* or *Euphausia pacifica*, accounted for over 75% of the total IRI for all years combined (Appendix Table 1). Fishes were more important, however, on a weight basis making up about 60% of the total biomass consumed. Juvenile rockfishes (*Sebastes* spp.), sandlance *Ammodytes hexapterus*, brown Irish lord *Hemilepidotus spinosus*, and greenlings (*Hexagrammos* spp.) were the dominant fish taxa identified. With the exception of barnacle cypris larvae and hyperiid amphipods which were quite numerous in stomachs collected at several stations, all other prey taxa were relatively unimportant. No relationship between predator and fish prey size was found ($n = 38$, $r = 0.19$, $p = 0.25$). However, steelhead, which had a smaller mean length than cutthroat trout, consumed a smaller mean size ($\bar{x}$ 35.9 mm TL, SD 16.6 mm) and size range (7–72 mm) of prey fishes than cutthroat trout.

The relative proportions by weight of the major prey categories varied substantially among the years sampled. Usually, fishes contributed the majority of the weight to the diet, but during the relatively strong upwelling years of 1982 and 1985 (Fisher and Pearcy 1988) euphausiids were more important. The largest number of prey categories occurred in steelhead and cutthroat stomachs during the relatively weak upwelling summers of 1981 and 1984.

The Percent Similarity Index between cutthroat trout and steelhead was 39% for all cruises combined.

Discussion

Cutthroat and steelhead trout have evolved contrasting migratory behavior in the ocean. Both species were absent in purse seine catches during September of their first summer in the ocean (Miller et al. 1983, Loch and Miller 1988; this paper), apparently because they migrated out of the coastal ocean. Cutthroat return to estuaries and freshwater streams from mid- to late summer (Giger 1972, Loch 1982), whereas most steelhead migrate far offshore during their first summer in the ocean (Hartt and Dell 1986).

Although some aspects of the life histories of cutthroat and steelhead trout are similar, their ecologies in marine waters differ. Steelhead commonly spend 2–3 years in the ocean and attain a large size before initiating their spawning migrations to freshwater. Some, however, return after only one full year in the ocean, and some return, though usually do not spawn, after several months in the ocean (Everest 1973). Apparently anadromous cutthroat trout return to freshwater after only a few months in coastal waters and rarely overwinter at sea. Giger (1972) did not identify any coastal cutthroat that had overwintered in the ocean, based on analyses of circuli patterns from scales of fish returning to coastal rivers of Oregon. Fish that migrated to sea in the spring invariably returned to freshwater in the summer or fall of the same year. Similarly, Armstrong (1971), Jones (1982) and Loch, and Miller (1988) did not report any cutthroat that spent an entire year in the ocean. J. Johnston (Wash. Dep. Wildl., Olympia, pers commun. 8 March 1990) found a few cutthroat trout in Hood Canal, WA, during February and March, fish that evidently overwintered in marine waters. Most cutthroat spawn after their return to freshwater, but according to Johnston (1982) a large percentage of the Columbia River, Puget Sound, British Columbia, and Alaska stocks of cutthroat overwinter but do not spawn in freshwater after their first summer in the ocean. Jones (1977) reported that less than 50% of the cutthroat migrating into Petersburg Creek in southeast Alaska were approaching sexual maturity. In some instances, coastal cutthroat may migrate downstream but not into the ocean. Smolts from the Cowlitz River in Washington may remain in the Columbia River estuary for a year (Tipping 1981 as cited by Johnston 1982), and some adults that

return to spawn in Sand Creek, OR, and Prairie Creek, CA, had no ocean growth on their scales (Sumner 1972, DeWitt 1954). Tomasson (1978) thought that coastal cutthroat did not migrate in large numbers beyond the Rogue River estuary.

Because coastal cutthroat only spend several months in the ocean, it is assumed that they inhabit waters close to the coast and not far from their homestream (Giger 1972). Johnston (1982) observed that anadromous cutthroat usually frequented waters less than 3 meters in depth in Puget Sound and that migration of tagged wild cutthroat did not extend much beyond 50 km from the home stream. However, cutthroat were caught by Loch and Miller (1988) up to 31.5 km offshore and within the Columbia River plume between Tillamook Bay, OR, and Willapa Bay, WA, suggesting more extensive offshore movements. Sumner (1972) also thought that cutthroat originating from the Columbia River basin may traverse along the coast within the Columbia River plume. Our data also suggest that some cutthroat undertake substantial movements along the coast (>250 km) and are found as far offshore (37–46 km) as the more oceanic steelhead smolts during the summer. One fish was caught 66 km offshore. Thus some individuals may reside far offshore along an open coast, as opposed to staying close to shore as they presumably do in protected inlets like Puget Sound (Johnston 1982). Straying of returning sea-run hatchery cutthroat trout is common (Bulkley 1966, Giger 1972, Jones 1977). Giger (1972) reported straying of marked hatchery cutthroat between the Nestucca, Siuslaw, and Alsea Rivers of the central Oregon coast. Most of the strays were recovered in rivers south of the river of release, possibly the result of advection by coastal currents during the early summer period of ocean residence, similar to that seen for coho salmon (Pearcy and Fisher 1988).

Giger (1972) noted a non-random distribution in the number of cutthroat smolts and kelts in seine samples in the Alsea estuary during the spring and "large schools" of sea-run fish in estuaries in the fall. He thought that anadromous cutthroat trout formed schools while at sea. However, we found no evidence of schooling from our limited ocean catches. Most cutthroat were caught singly. To our knowledge, schooling of cutthroat or steelhead trout in the ocean has not been documented.

Steelhead migrate long distances into oceanic waters and are widely distributed in the North Pacific Ocean based on catches of marked and unmarked fish (Sutherland 1973; Pearcy and Masuda 1982, 1987; Okazaki 1983; Hartt and Dell 1986; Light et al. 1988). Miller et al. (1983) found that juvenile steelhead caught in purse seines between Tillamook Bay and Willapa Bay occurred farther offshore than juvenile coho or chinook salmon and migrated out of the coastal sampling area early in the summer. Purse seining and tagging studies by Hartt and Dell (1986) from Cape Flattery, WA, to the Aleutian Islands clearly showed that juvenile steelhead migrate directly offshore rather than along a coastal belt where other juvenile salmonids typically migrate. Recovery of steelhead during their first summer in the ocean in the Gulf of Alaska confirms rapid migrations of some fish into oceanic waters far from land. Pearcy and Masuda (1982) report on a steelhead captured over 1600 km from land only a few months after its initial ocean entry.

These conclusions of immediate migrations of steelhead offshore and into subarctic waters of the North Pacific after ocean entry, and residence in oceanic waters during their first winter in the ocean, do not apply to all steelhead. Most steelhead from the Rogue River in Oregon (the "half-pounder" runs) return to freshwater after only a few months following their initial migration to the ocean (Everest 1973), and likely do not migrate very far in the ocean. The recovery of marked Rogue River summer steelhead south of the Rogue River (Everest 1973), and the rarity of marked steelhead originating from streams south of Cape Blanco in waters to the north of Cape Blanco in our catches, suggest that these steelhead from the southern extremity of their range may not migrate to the north after ocean entry. This conclusion is supported by the high seas distribution of tagged steelhead. Although 9 tagged steelhead from California and 11 from Oregon streams have been recovered north of 45°N in the northeastern Pacific, only 3 fish with coded-wire tags from California have been recovered at sea of the over 1 million coded-wire tagged steelhead released between 1980 and 1985, and only one was caught north of California (Light et al. 1988, Pacific States Marine Fisheries Comm. unpubl.). Possibly southern steelhead reside in the strong upwelling zone off northern California and southern Oregon (Bakun 1975).

The feeding habits of juvenile steelhead and cutthroat trout in estuaries and in coastal waters are similar. Both species feed intensively on gammarid amphipods and insects in estuaries on their initial migration to the sea, but steelhead smolts also eat the benthic mollusk *Corbicula* (Loch 1982, McCabe et al. 1983, Bottom et al. 1984). During their early residence in waters along the open coast, cutthroat trout feed primarily on fishes (Armstrong 1971, Fresh et al. 1981, Brodeur et al. 1987a, Loch and Miller 1988, this paper). We found that steelhead trout also consumed fish but had a more varied diet than cutthroat trout. Euphausiids and other crustaceans were important in the diet of steelhead trout, especially during the strong upwelling years of our study when euphausiids may have been abundant (Brodeur 1986). Many prey species identified in the

diets of the trout species (juvenile rockfishes, hexagrammids, anchovy, *Cancer* spp. megalopae, and insects) are commonly found in the neustonic layer (Brodeur et al. 1987b, Shenker 1988) which suggests that these trouts feed in surface waters. The occurrence of a juvenile salmon in the diet of juvenile cutthroat is noteworthy since larger individuals (>300 mm) of this species were identified as one of the few fish predators on juvenile salmonids among the 20 species of nekton examined from these same purse seine catches (Brodeur et al. 1987a).

Dietary overlap of 39% between cutthroat and steelhead trout based on percent similarity was higher than the overlap values between these species of trout and the juveniles of four species of salmon caught in purse seines, with two exceptions. The highest overlap values were between cutthroat trout and juvenile chinook salmon (49%) because of the common utilization of fishes in the diet, and between juvenile steelhead trout and juvenile sockeye salmon (43%) because of the common occurrence of euphausiids.

The average growth rate of cutthroat trout in the ocean based on our scale analysis was 0.8 and 1.0 mm/day (based on 1 May and 10 May dates of ocean entry, respectively) and 1.2 mm/day (based on change in back-calculated ocean growth with time). These estimates are similar to the growth rates of about 1.0 mm/day for age 2. wild cutthroat and 0.9 mm/day for hatchery cutthroat, assuming a 3-month ocean residence (Giger 1972) and 0.7–0.8 mm/day for fish after their first 5–6 months in the ocean (Sumner 1962). Johnston (1982) reported an average growth rate of 1.0 mm/day during the time spent at sea for cutthroat trout stocks from the Columbia River, coastal rivers, and Puget Sound rivers. Our average growth rate for steelhead of 1.1 mm/day (based on a 17 May date of ocean entrance) is similar to that for cutthroat trout. It is about the same as the average ocean growth of 1.3 mm/day calculated by Everest (1973), the 0.8 mm/day estimated by K. Kenaston (Oreg. Dep. Fish Wildl., Corvallis, pers. commun. 16 June 1989) for summer-run steelhead "half-pounders" of the Rogue River, and the 1.5 mm/day estimated for first-year ocean growth of steelhead from Vancouver Island (Hooten et al. 1987). Data on ocean growth of steelhead during their first year in the ocean is also provided by recovery of fish with coded-wire tags. These include growth rates of about 1.0 mm/day for a fish caught in the Gulf of Alaska, based on the mean size of the same tag code of steelhead smolts when caught about 60 days earlier in the Columbia River (Pearcy and Masuda 1982), and growth rates of 0.7, 1.0, and 1.2 mm/day for coded-wire tagged steelhead recovered 198, 186, and 173 days, respectively, after release (Pacific States Marine Fisheries Comm. unpubl.). Lengths at release were estimated from release weight using the length-weight relationships for steelhead smolts given by Everest (1973). The average growth rate of steelhead during their first full year in the ocean was about 1.0 mm/day for fish returning to California streams (calculated from data in Shapovalov and Taft 1954), 0.6 mm/day for fish caught on the high seas (Sutherland 1973), and 0.85 mm/day for fish from the Keogh River, British Columbia (Ward and Slaney 1988). These estimates suggest fairly similar growth rates for both cutthroat and steelhead trout during early ocean life. Apparently cutthroat trout are small when they return to spawn because they spend less time in the ocean, not because of an inherently lower growth rate.

If coastal cutthroat trout have the potential for a large increase in size during ocean life, why do they curtail marine growth by returning to freshwater each winter rather than remaining in the ocean for several years like most steelhead trout? We present three hypotheses for the adaptive value of this behavior.

Early maturation of cutthroat trout, after only a few months in the ocean, may have evolved as a response to low survival (Cole 1954), either in the ocean or freshwater, especially if postreproductive survival is low after the age at first breeding (Schaffer 1974). Cutthroat trout do not appear to have distinctly lower ocean survival than steelhead, however, based upon the reports in literature. Giger (1972) states that coastal cutthroat exhibited comparatively high rates of survival during summer periods of ocean residence between spawnings. He estimated ocean survival rates of 20–40% for hatchery cutthroat smolts between release in the spring and return in the fall, and survival rates of 14–39%, 17–35%, and 12–25% between first and second, second and third, and third and fourth spawnings, respectively, based on trap or net catches of fish returning to four Oregon coastal streams. Sumner (1962) estimated that 17–50% of coastal cutthroat trout survived between successive spawnings, and Jones (1978) reported marine survival of 17%. Tomasson (1978), on the other hand, noted that 92% of the fish returning to the Rogue River were first migrants, suggesting low survival of repeat spawners, and Michael (1983, 1989) reported marine survival rates of 2–20% between smolt outmigration and first return to freshwater for coastal cutthroat trout.

Cutthroat survival to an ocean age of 2, the age when many steelhead trout return for their initial spawning (Withler 1966, Shapovalov and Taft 1954, Chapman 1958), is about 5% (assuming 20% survival from smolt to first spawning and 25% survival from first to second spawning, based on Giger's estimates), a value which is close to the average for smolt to adult return for steelhead (Bley and Moring 1988), but less than the mean ocean survival of 16% based on maiden-run fish

given by Ward and Slaney (1988). Thus survival rates to ocean age 2 of these two species appear to be roughly similar, as is survival of repeat spawners of cutthroat trout and steelhead trout (Giger 1972, Withler 1966, Ward and Slaney 1988). Lower ocean survival or lower postreproductive survival of cutthroat trout than steelhead may not be a cogent explanation for cutthroat trout spawning at an early age and small size.

The second hypothesis is that small size at maturity in cutthroat trout relative to steelhead trout may have evolved as a result of the distance and rigor of spawning migrations. Schaffer and Elson (1975) concluded that the mean age of first spawning of Atlantic salmon increased with the difficulty of upstream migration, as estimated by the distance ascended into freshwater. Coastal cutthroat rarely penetrate inland more than 160 km (Johnston 1982), and hence may not need the swimming performance or energy reserves required for the long and arduous upstream migrations that some steelhead undertake at the time of maturity.

Finally, the small size at maturity attained by cutthroat trout may permit utilization of small, shallow tributaries for spawning and rearing where interspecific competition with other anadromous salmonids is reduced. Small streams are known to be important spawning and rearing areas of cutthroat trout (DeWitt 1954, Needham and Gard 1959, Lowry 1965, Johnston 1982, Trotter 1989). Sea-run cutthroat trout generally spawn in tributaries with a lower velocity and shallower depth than steelhead (Hunter 1973). Hartman and Gill (1968) reported that where both anadromous cutthroat trout and steelhead were sympatric, juvenile cutthroat were predominant in headwater tributaries and steelhead in larger river reaches. Cutthroat trout are behaviorally subordinate to steelhead and coho salmon in agonistic encounters (Nilsson and Northcote 1981, Glova 1986, Griffith 1988) and their populations appear to be suppressed by competition from anadromous salmonids (R. House, Unpubl.). The lack of morphological specialization of cutthroat trout to either fast or slow water may be another reason why this species is dominated by coho salmon and steelhead in areas of sympatry (Bisson et al. 1988). Anadromous cutthroat are known to penetrate, spawn, and rear farther into a watershed than steelhead trout (Michael 1983), sometimes above natural falls or log jams (Mitchell 1988; R. House, Unpubl.) that were considered to be barriers to anadromous salmonids (see Michael 1983). Therefore, small size at maturity may be adaptive by allowing anadromous cutthroat trout to spawn and rear in numerous small tributaries of coastal streams where other salmonids are absent or less abundant.

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Appendix Table 1

Percent frequency occurrence (F), percent number (N), percent weight (W), and percent index of relative importance (IRI) of food items in juvenile steelhead and cutthroat trout stomachs for all years combined. Values in parentheses are summaries by major taxonomic categories.

	Steelhead trout				Cutthroat trout			
Prey taxa	F	N	W	IRI	F	N	W	IRI
Cnidaria								
Velella velella	1.1	<0.1	0.1	<0.1	–	–	–	–
Siphonophora								
Unidentified	1.1	<0.1	<0.1	<0.1	–	–	–	–
Annelida								
Tomopteris septentrionalis	1.1	<0.1	<0.1	<0.1	–	–	–	–
Tomopteris spp.	1.1	<0.1	<0.1	<0.1	–	–	–	–
Mollusca								
Gastropoda								
Limacina helicina	1.1	4.8	0.1	0.1	3.2	0.5	0.1	<0.1
Cephalopoda								
Loligo opalescens	1.1	<0.1	<0.1	<0.1	–	–	–	–
Unidentified	1.1	<0.1	0.1	<0.1	–	–	–	–
Arthropoda								
Copepoda	(4.2)	(4.0)	(0.1)					
Neocalanus cristatus	1.1	0.1	<0.1	<0.1	–	–	–	–
Epilabidocera longipedata	1.1	<0.1	<0.1	<0.1	–	–	–	–
Euchaeta elongata	1.1	3.9	<0.1	0.1	–	–	–	–
Unidentified	1.1	<0.1	<0.1	<0.1	–	–	–	–
Cirripedia								
Unidentified cypris	18.1	9.6	0.5	3.4	–	–	–	–
Unidentified remains	6.4	0.4	1.1	0.2				
Isopoda								
Gnorimosphaeroma oregonensis	1.1	0.1	<0.1	<0.1		–	–	–
Idotea fewkesi	–	–	–	–	1.6	<0.1	0.1	<0.1
Amphipoda	(29.5)	(5.1)	(1.6)					
Calliopeia laeviusculus	1.1	<0.1	<0.1	<0.1		–	–	–
Unidentified Gammaridea	1.1	<0.1	<0.1	<0.1		–	–	–
Hyperoche medusarum	3.2	0.1	0.3	<0.1	–	–	–	–
Hyperoche medusarum	21.3	2.2	1.0	1.3	6.5	0.7	0.1	0.1
Themisto pacifica	3.2	2.7	<0.1	<0.1	1.6	<0.1	0.1	<0.1
Brachyscelus crusculum	1.1	<0.1	0.1	<0.1	–	–	–	–
Unidentified Hyperiidea	2.1	0.1	0.1	<0.1	1.6	0.2	<0.1	<0.1
Caprella mexa	1.1	<0.1	<0.1	<0.1	–		–	
Euphausiacea	(67.4)	(54.1)	(32.7)		(24.2)	(16.0)	(2.0)	
Euphausia pacifica	43.6	8.3	12.0	16.4	8.1	0.5	0.4	0.2
Nematoscelis difficilis					1.6	0.1	0.1	<0.1
Thysanoessa spinifera	50.0	43.9	19.8	58.8	9.7	9.4	0.2	2.4
Thysanoessa raschii	1.1	1.3	<0.1	<0.1	–	–	–	–
Nyctiphanes simplex	1.1	0.1	<0.1	<0.1	–		–	
Unidentified furcilia	1.1	<0.1	<0.1	<0.1	–	–		
Unidentified	12.8	0.5	0.9	0.3	8.1	6.0	1.3	1.5

Appendix Table 1 (continued)

Prey taxa	Steelhead trout F	N	W	IRI	Cutthroat trout F	N	W	IRI
Euphausiacea (continued)								
Decapoda	(14.7)	(5.6)	(1.9)		(17.7)	(4.9)	(1.4)	
Crangon spp. zoea	–	–	–	–	1.6	0.5	<0.1	<0.1
Pagurus spp. zoea	–	–	–	–	1.6	<0.1	<0.1	<0.1
Pagurus spp. megalopae	–	–	–	–	1.6	0.5	<0.1	<0.1
Porcellanidae megalopae	–	–	–	–	1.6	0.5	<0.1	<0.1
Pugettia producta zoea	–	–	–	–	3.2	0.1	<0.1	<0.1
Cancer antennarius megalopae	2.1	<0.1	<0.1	<0.1	1.6	0.1	<0.1	<0.1
Cancer magister megalopae	8.5	0.5	1.4	0.3	12.9	2.9	1.3	1.4
Cancer oregonensis megalopae	5.3	2.4	0.4	0.3	3.2	0.1	<0.1	<0.1
Cancer spp. zoea	2.1	2.7	<0.1	0.1	1.6	<0.1	<0.1	<0.1
Pinnotheridea megalopae	–	–	–	–	1.6	<0.1	<0.1	<0.1
Unidentified larvae	1.1	<0.1	<0.1	<0.1	1.6	<0.1	<0.1	<0.1
Insecta	(8.4)	(0.2)	(0.2)		(8.1)	(1.2)	(0.8)	
Choristoneura occidentalis	1.1	<0.1	<0.1	<0.1	–	–	–	–
Hymenoptera	–	–	–	–	3.2	0.7	0.6	0.1
Coleoptera	1.1	<0.1	<0.1	<0.1	–	–	–	–
Hemerobiidae	1.1	<0.1	<0.1	<0.1	–	–	–	–
Diptera	2.1	<0.1	<0.1	<0.1	1.6	<0.1	<0.1	<0.1
Unidentified	5.3	0.1	0.1	<0.1	6.4	0.5	0.2	0.1
Chordata								
Osteichthyes	(70.5)	(16.0)	(61.4)		(87.1)	(76.2)	(95.1)	
Clupea harengus pallasi	4.2	0.1	2.4	0.2	–	–	–	–
Engraulis mordax	–	–	–	–	9.7	1.3	7.8	2.3
Allosmerus elongatus	1.1	0.1	3.7	0.1	–	–	–	–
Spirinchus thaleichthys	–	–	–	–	1.6	0.1	3.7	0.2
Osmeridae	1.1	<0.1	0.1	<0.1	3.2	0.1	6.6	0.6
Oncorhynchus sp.	–	–	–	–	1.6	0.1	2.0	0.1
Sebastes flavidus	–	–	–	–	1.6	0.1	1.4	0.1
Sebastes jordani	1.1	<0.1	1.2	<0.1	–	–	–	–
Sebastes spp.	21.3	0.4	22.5	9.0	11.3	5.0	7.9	3.8
Anoplopoma fimbria	2.1	0.1	0.1	<0.1	1.6	<0.1	0.9	<0.1
Hexagrammos decagrammus	2.1	0.1	1.8	0.1	9.7	0.7	16.7	4.3
Hexagrammos spp.	4.3	0.1	4.9	0.4	8.1	27.7	7.6	7.3
Ophiodon elongatus	3.2	<0.1	0.9	0.1	3.2	0.1	0.9	0.1
Agonidae	1.1	1.3	<0.1	<0.1	–	–	–	–
Hemilepidotus spinosus	7.4	0.2	4.3	0.6	12.9	0.9	7.4	2.7
Scorpaenichthys marmoratus	3.2	0.1	0.1	<0.1	4.8	4.8	5.2	1.2
Cottidae	3.2	5.3	0.1	0.3	–	–	–	
Ammodytes hexapterus	10.6	1.6	3.3	1.0	9.7	0.6	2.9	0.9
Ronquilus jordani	1.1	1.3	0.1	<0.1	–	–	–	–
Citharichthys sordidus	1.1	<0.1	0.4	<0.1	–	–	–	–
Psettichthys melanostictus	1.1	0.1	0.8	<0.1	–	–	–	–
Unidentified larvae	13.8	0.5	2.4	0.7	4.8	0.3	0.5	0.1
Unidentified juveniles	8.5	1.5	4.4	0.9	16.1	0.8	10.6	4.7
Unidentified remains	24.5	3.1	7.9	5.0	54.8	33.6	13.0	65.6
Plant material	2.1	<0.1	0.1	<0.1	1.6	<0.1	0.5	<0.1
Number of stomachs examined		98				67		
Number of empty stomachs		4				5		
Mean fork length (mm)		213.4				254.5		
Fork length range (mm)		158–294				162–298		

Abstract.– Spiny lobsters *Panulirus marginatus* from the Hawaiian Archipelago have undergone heavy fishing pressure since 1980 and have experienced increases in asymptotic length and decreases in mean length at onset of egg production. Prior to the expansion of the fishery, allozyme variation was surveyed, and populations were found to be polymorphic at seven loci. In 1987 we collected spiny lobsters from two of the previously sampled locations (Necker Island and Maro Reef) to test for significant changes in population structure or level of genetic variability. No significant changes through time were found at five of the seven loci. Significant differences were detected at *Est3* and *EstD*; however, frequencies at esterase loci have been previously shown to fluctuate through time. Observed number of allelic classes and observed heterozygosities have remained unchanged. The data suggest that no change in the amount of variability has occurred in spiny lobster since the expansion of the fishery.

Genetic Variation in Highly Exploited Spiny Lobster *Panulirus marginatus* Populations from the Hawaiian Archipelago

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Commercial trapping for the spiny lobster *Panulirus marginatus* in the northwestern Hawaiian Islands began in 1976 shortly after research cruises documented the resource in abundance. Two banks, Necker Island and Maro Reef, have been most heavily fished since the beginning of the fishery. In 1986 and 1987 research cruises repeated the earlier sampling at Necker Island and Maro Reef by trapping at the same sites on each bank with the same gear to document any changes that had occurred in density, population, and genetic parameters (Polovina 1989). The repeat sampling documented substantially reduced lobster densities as indicated by catch rates, which in 1986–87 were 37% and 68% of their 1977 levels at Necker Island and Maro Reef, respectively (Polovina 1989). A statistically significant ($P<0.05$) increase in the asymptotic lengths and decreases in the mean lengths at onset of egg production occurred between the 1977 and 1986–87 sampling at both locations (Polovina 1989).

While changes in these population parameters could be due to density-dependence relationships, some type of genetic change also may have occurred from selection induced by the fishing pressure (Nelson and Soulé 1987). For example, the fishery harvests lobsters at about the size the females first begin producing eggs. It is estimated that spiny lobster enter the fishery at 3.1 years of age and that the mean age females begin producing eggs is 2.5 years (Polovina 1989). Thus, heavy fishing pressure may select for female lobsters that sexually mature at a smaller size. Reduction in the total amount of genetic diversity or changes in the stock structure of the exploited populations are also potential results of intense fishing pressure (Allendorf et al. 1987). These latter types of genetic changes can often be monitored through allozyme analyses (Nelson and Soulé 1987), and are the subject of this paper.

Spiny lobsters from seven localities in the Hawaiian Archipelago were collected between 1978 and 1980, prior to the expansion of the commercial fishery, and analyzed for allozyme variation by Shaklee and Samollow (1984). Although overall levels of variation were quite low, they observed polymorphism at 7 of the 46 loci examined. However, no clear pattern of genetic differentia-

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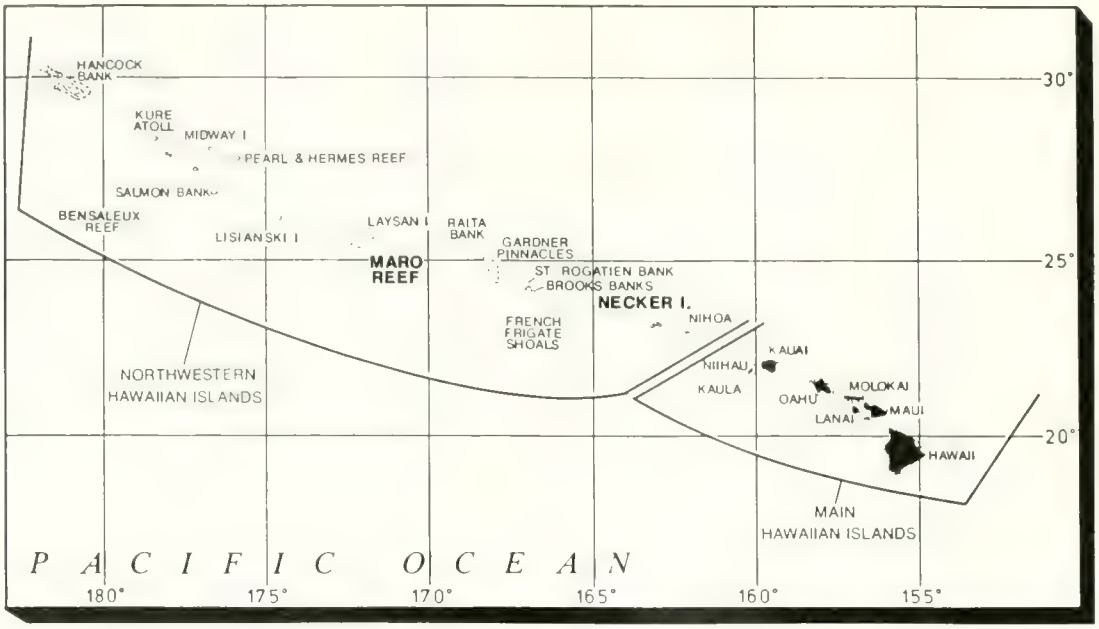

Figure 1
Location of Maro Reef and Necker Island within the Hawaiian Archipelago.

tion among populations was detected, and they concluded that a single panmictic stock of spiny lobster exists throughout the Hawaiian Archipelago.

Our objective was to reexamine allozyme variation at those seven loci to determine if fishing pressure since 1980 affected population structure or genetic variability. During 1987, new collections of spiny lobsters from two of the same localities in the northwestern Hawaiian Islands (Maro Reef and Necker Island) were made. These two sites represent the mainstay of the commercial fishery. They are the most productive banks, have been fished the longest, and annually receive the greatest fishing pressure.

Analysis showed that the observed number of allelic classes and observed heterozygosity have remained essentially unchanged between 1978 and 1987. These data provide no evidence that population bottlenecks have occurred. Fishing pressure since 1980 has not reduced the genetic variability as detected by protein electrophoresis in spiny lobster from either of these two sites in the northwestern Hawaiian Islands.

Methods and materials

Muscle and digestive gland from 200 specimens from Maro Reef and Necker Island (Fig. 1) were collected, frozen onboard ship, and shipped frozen to the laboratory for analysis. Upon receipt, tissues were subsampled for electrophoresis and stored at −80°C for up to 4 weeks while analysis was completed.

Electrophoretic methods generally followed May et al. (1979) and Shaklee and Samollow (1984) to facilitate comparison. Samples were analyzed for the products of seven loci previously identified as polymorphic: *Est3*, Esterase, E.C. 3.1.1.–; *EstD* (*Umb*), Esterase, E.C. 3.1.–.–, resolved with 4-methylumbelliferyl acetate; *Gpi*, glucosephosphate-6-isomerase, E.C. 5.3.1.9; *Mpi*, mannose-6-phosphate isomerase, E.C. 5.3.1.8; *Pgm*, phosphoglucomutase, E.C. 5.4.4.2; *Tpep1,2* (*Pep-1,2*), tripeptidase aminopeptidase, E.C. 3.4.–.–, resolved with L-leucyl-L-leucyl-L-leucine. However, in contrast to the methods of Shaklee and Samollow (1984) who used horizontal and vertical gels, all analyses were performed on horizontal starch gels. *Tpep1* was resolved on an additional buffer, amine-citrate gel and tray buffer, pH 6.9 (Clayton and Tretiak 1972).

The electrophoretic data were analyzed using BIOSYS-1 (Swofford and Selander 1981). Allelic classes followed those of Shaklee and Samollow (1984), who pooled alleles into f(fast), m(medium), and s(slow) classes for numerical analyses. Pooling was required in their study and ours because many alleles were too rare to include in the statistical tests. Actual mobilities observed were also recorded.

Comparisons between the 1978–80 and 1987 data sets for each reef were performed using a chi-square contingency analysis based on the number observed in

Table 1

Allele frequencies for seven polymorphic loci in the spiny lobster *Panulirus marginatus*. Data from 1978–80 are those of Shaklee and Samollow (1984). Alleles are identified by relative mobility classes assigned by Shaklee and Samollow (1984). Actual mobilities observed in this study are also given. Numbers of individuals successfully scored are given in parenthesis.

	Est3			*EstD*			*Gpi*			
Location and date	f	m 100	s 93	f	m 100	s	f 100	m 88	s 66	ff 145
Maro Reef										
1978–80	0.003	0.957 (386)	0.040	0.001	0.988 (340)	0.010	0.959	0.039 (320)	0.002	—
1987	—	0.968 (174)	0.032	—	1.000 (199)	—	0.970	— (198)	0.028	0.003
Necker Island										
1978–80	—	0.971 (666)	0.030	0.011	0.980 (533)	0.008	0.966	0.033 (535)	0.001	—
1987	—	0.992 (194)	0.008	—	1.000 (200)	—	0.955	0.002 (200)	0.020	0.022

	Mpi		*Pgm*			*Tpep1*		*Tpep2*		
	f 101	f+s 96, 100	f 200	m 100	s −33 −66	f 100	s 66	f ***	m 100	s 89
Maro Reef										
1978–80	0.011	0.989 (418)	0.007	0.984 (345)	0.009	0.725	0.275 (142)	—	0.988 (335)	0.012
1987	0.005	0.995 (193)	0.003	0.977 (198)	0.020	0.768	0.232 (179)	0.006	0.975 (180)	0.019
Necker Island										
1978–80	0.007	0.993 (649)	0.007	0.976 (558)	0.017	0.785	0.215 (142)	0.001	0.984 (425)	0.015
1987	0.003	0.998 (188)	-	0.985 (200)	0.014	0.768	0.232 (144)	—	0.980 (176)	0.020

each allelic class. Shaklee and Samollow (1984) found no heterogeneity between year classes for any loci except *EstD*, and thus they report pooled frequencies. They provide annual frequency estimates for *EstD* for 1979 and 1980.

We also compared the 1987 data sets from Maro Reef and Necker Island using chi-square contingency analysis.

Results

Allozyme analysis

All loci previously observed to be polymorphic were also found to be variable in the new samples, with the exception of *EstD* (Table 1). Allele classes observed by Shaklee and Samollow (1984) and not observed in this study were *Est3(f)*, *EstD(f)*, and *EstD(s)*. We observed *Gpi(145)* in both populations; this allele was not previously reported. Additionally, when analyzing *Tpep1* allozymes, we detected a *Tpep3(94)* allele in a single individual from Maro Reef which was not observed previously. Isozyme patterns agreed with descriptions provided in the earlier study. There were no indications of non-genetic variation at the esterase or any of the other loci.

Genotypic frequencies at all loci fit the expectation of Hardy-Weinberg equilibrium with the exception of *Est3* in Maro Reef ($P = 0.041$) and *Mpi* in both populations. *Mpi* has an unusual distribution of alleles between the two sexes (Shaklee 1983). Males always carry at least one slow allele, while females rarely have this variant. The common and slow variant alleles were pooled for the statistical analyses, and only the frequency of the fast allele is reported. With pooling, a test for fit to Hardy-Weinberg is possible, and no significant deviation from Hardy-Weinberg was observed.

Table 2

Average per locus and mean heterozygosity over all loci for spiny lobster *Panulirus marginatus* from Maro Reef and Necker Island.

Location and date	*Est3*	*EstD*	*Gpi*	*Mpi*[1]	*Pgm*	*Tpep1*	*Tpep2*	Mean[2]
Maro Reef								
1987	0.061	0.000	0.059	0.381	0.045	0.356	0.049	0.021
Necker Island								
1987	0.015	0.000	0.087	0.477	0.030	0.389	0.039	0.023
Hawaiian Archipelago								
1978–80[3]	0.059	0.032	0.076	0.374	0.042	0.370	0.026	0.021

[1] Sex restricted allele distribution (Shaklee 1983).
[2] 1987 estimate assumes monomorphism at the 39 additional loci surveyed by Shaklee and Samollow (1984).
[3] From Shaklee and Samollow (1984).

Chi-square analyses

Contingency chi-square analyses were performed between the two newly sampled collections at each of the polymorphic loci. Because of their low frequencies, all variant alleles at each locus were pooled into one class. Significant heterogeneity between Necker Island and Maro Reef was observed for *Est3* ($\chi^2 = 5.61$, df = 1, $P<0.020$).

Contingency chi-square analyses were also performed between the data gathered in this study and those of Shaklee and Samollow (1984) at each of the polymorphic loci. Significant heterogeneity was observed between the Necker Island 1987 and 1979–80 collections at *Est3* ($\chi^2 = 5.86$, df = 1, $P<0.025$).

Shaklee and Samollow (1984) reported fluctuating frequencies over years at the *EstD* locus and concluded that the 1980 samples represented a cohort with an unusual frequency. Therefore, we tested for heterogeneity between our data and the 1979 and 1980 *EstD* data separately. Both Maro Reef and Necker Island were significantly different for the 1980 comparison (Maro Reef, $\chi^2 = 9.71$, df = 1, $P<0.005$; Necker Island, $\chi^2 = 15.42$, df = 1, $P<0.001$). The Necker Island 1987 data were significantly different from the 1979 data ($\chi^2 = 6.10$, df = 1, $P<0.02$); the Maro Reef data were not significantly different.

Number of allelic classes

The total number of observed alleles at all sampled loci can also be used as an indicator of overall variability. Shaklee and Samollow (1984) observed a total of 18 different allelic classes in both the Maro Reef and Necker Island collections; we observed, for the same loci, 16 and 15 classes, respectively (Table 1). Although three classes (with frequencies of 0.010 or less) detected earlier were not observed in this study, two new alleles were observed.

It is also important to note the persistence of low-frequency allelic classes. *Gpi(s)*, *Pgm(f)*, and *Pgm(s)* were present in the 1978–80 Maro Reef collections at frequencies of 0.009 or less; all were present in the 1987 collection. *Gpi(s)* and *Mpi(f)* were present in the 1978–80 Necker Island collection at frequencies of 0.007 or less; both were present in the 1987 collection.

Heterozygosity

Heterozygosities were calculated for each locus for each population (Table 2). The *Est3* heterozygosities in the 1987 Necker Island collection were lower than those observed in the Hawaiian Archipelago during 1978–80 as no variants at this locus were observed. However, the 1987 Necker Island average heterozygosity over all loci was 0.023 (assuming monomorphism for the 39 additional loci previously resolved) compared with the value of 0.021 reported in the earlier study. Mean heterozygosities were statistically indistinguishable between the two populations and those observed in the earlier study. It should be noted, though, that differences on the order of 5% heterozygosities may require that large numbers of loci be screened to statistically test significant differences, and tests of heterozygosities are particularly insensitive when comparing low levels of heterozygosity such as observed in this study (Archie 1985).

Discussion

Stability of allele frequencies over at least 7 years was found at *Gpi*, *Mpi*, *Pgm*, *Tpep1*, and *Tpep2*. The gene frequencies of spiny lobster from Maro Reef and Necker Island appear to be stable both between collection sites and between years at all loci, with the exception of the two esterase loci. The variability at

the two esterase loci is of particular concern. Is this variability indeed indicative of genetic isolation between the two sampling localities or of changes in the stock structure?

The data of Shaklee and Samollow (1984) showed that *EstD* allele frequencies fluctuate in spiny lobster. They detected annual significant fluctuations in allele frequency within localities, but these annual fluctuations were parallel among Maro Reef, Necker Island, and an additional locality, Kure Atoll. Thus, the fluctuating frequencies did not lead to any significant differences in allele frequency between localities within years.

Our data, 7 years later, are somewhat consistent with this pattern for *EstD*. We detected significant differences between years, but no significant differences were found between localities sampled the same year. These data support the contention that fluctuations in the northwestern Hawaiian Islands do occur in *EstD* allelic frequencies. The data are insufficient to warrant invoking selection or drift as an explanation; however, one suitable hypothesis might be that these fluctuations were caused by immigration of a closely related population differing only at *EstD* frequencies.

However, unlike the previous data set, our data show a significant difference between the 1987 Necker Island and Maro Reef collections at *Est3*. Such change at a single locus could indicate either selection or stochastic processes operating on the *Est3* allelic frequencies with a lack of gene flow between the two localities.

No significant differences in levels of heterozygosity were detectable. This finding is not surprising. The rate of change in heterozygosity based on random drift is inversely proportional to population size (Hartl and Clark 1989) and is calculated as

$$H_t = (1 - 1/2N)^t H_0$$

where H_0 is the original heterozygosity value, H_t is the heterozygosity value after t generations, and N is the population size. At most, four generations have passed since the previous sampling. Thus, heterozygosity values should be indistinguishable with population sizes characteristic of a commercially exploitable species.

An analysis of low-frequency or rare alleles is often a more sensitive test to detect changes in variability. We observed a number of low-frequency alleles that were previously detected by Shaklee and Samollow (1984). Gregorius (1980) estimates that a sample size of 754 or greater would be needed to assure a 95% probability of detecting all alleles at a locus with frequencies of 0.01 or greater. Sample sizes were large in the earlier study—ranging from 386 to 666—increasing the probability of detection of rare alleles. Thus, it was expected that some of the previously detected rare alleles would not be observed in the 1987 collections, where sample sizes were 200 or less. Our data suggest that there has been no overall reduction in number of rare alleles within the populations; in fact, we detected rare alleles that were previously undetected.

The unchanged average heterozygosities and the persistence of rare alleles indicate that there has been no measurable loss of genetic variability due to fishing pressure. An additional concern in the management of the lobster fishery is whether each bank is primarily a self-recruiting population with minimal larval recruitment coming from other banks, or whether larval recruitment at any bank comes from an archipelago-wide gyre so the depletion of the spawning stock at any one bank will not affect recruitment to that bank. The significant difference between the 1987 Necker Island and Maro Reef frequencies at *Est3* is consistent with the hypothesis that the banks are largely self-recruiting, although this locus also appears to have varied significantly over time. Additional genetic studies, possibly including more sensitive DNA markers, are warranted to further elucidate the amount of genetic differentiation between these two important lobster populations. At present, though, a conservative management strategy would be based on the existence of two self-recruiting populations rather than a strategy based on a single panmictic unit.

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Abstract.—The impact of oil and gas development on fish populations off Louisiana is presumed significant but poorly understood. This study was undertaken to determine the applicability of a logbook program in developing a long-term database of species composition and relative abundance of fish associated with oil and gas structures. A pilot logbook program involving 120 private vessel owners and 25 charterboat operators was conducted between March 1987 and December 1988. Participants recorded date, fishing time, fishing method, number of anglers, and catch composition at each structure fished. Logbooks from a total of 55 private vessel owners and 10 charterboat operators were used in the analysis. Data collected included 15780 angler hours of fishing effort and 61227 fish caught over the study period. A total of 1719 trips were made to 589 different oil and gas structures with at least 46 different species of fish caught. Red snapper and spotted seatrout were the most commonly caught species and had the highest catch rates. Results differed from past logbook programs and creel surveys, possibly indicating a change in the community of fish associated with oil and gas structures.

A Fishery-dependent Based Study of Fish Species Composition and Associated Catch Rates Around Oil and Gas Structures Off Louisiana*

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Louisiana has long been revered as a "Sportsman's Paradise" and justifiably so, as evidenced by the abundant recreational fishing opportunities. A contributing factor to this "paradise" is the large number of oil and gas platforms acting as defacto artificial reefs. There are approximately 3700 oil and gas structures that constitute 28% of the known hard substrate off Louisiana and Texas (Gallaway 1984). Since the nearest natural hardbottom habitat is approximately 92 km off the Louisiana coast (Sonnier et al. 1976), oil and gas platforms provide the only source of hardbottom habitat (i.e., artificial reefs) close to shore.

Oil and gas platforms are unique as artificial reefs because they extend throughout the entire water column. Due to the size and shape of the structures they are thought to affect benthic, demersal, and pelagic fishes (Gallaway et al. 1981, Continental Shelf Associates 1982). Pelagic baitfish (i.e., round scad *Decaptarus punctatus*, Spanish sardine *Sardinella anchovia*, and scaled sardine *Harengula pensacolae*) often maintain a position from near the surface to mid-depth within or upcurrent from oil and gas structures, while large predatory pelagic fishes (i.e., king mackerel *Scombermorous cavalla*, and blue runner *Caranx crysos*) were reported to swim from the surface to mid-depth around structures (Hastings et al. 1976, Gallaway et al. 1981).

Evidence for the success of platforms as artificial reefs comes from sportfishing which is concentrated around these structures off the coast of Louisiana. An estimated 37% of the total saltwater angling effort and over 70% of all recreational angling trips that venture into the Exclusive Economic Zone (more the 3 miles from shore) off Louisiana occur around platforms (Witzig 1986, Reggio 1987).

In general there is little known about the species associated with oil and gas structures. Reported catch composition of charter boat operators fishing oil and gas platforms included (unranked): snapper (Family Lutjanidae), seatrout *Cynoscion* sp., Atlantic croaker *Micropogonias undulatus*, red drum *Sciaenops ocellatus*, king mackerel, cobia *Rachycentron canadum*, bluefish *Pomatomus saltatrix*, and sharks (Order: Selachii) based on studies by Dugas et al. (1979) and Ditton and Auyong (1984). Similar catch compositions were reported for private vessel anglers (Ditton and Auyong 1984, Stanley and Wilson 1989). In general, bottom fishing was reported to be the predominant fish-

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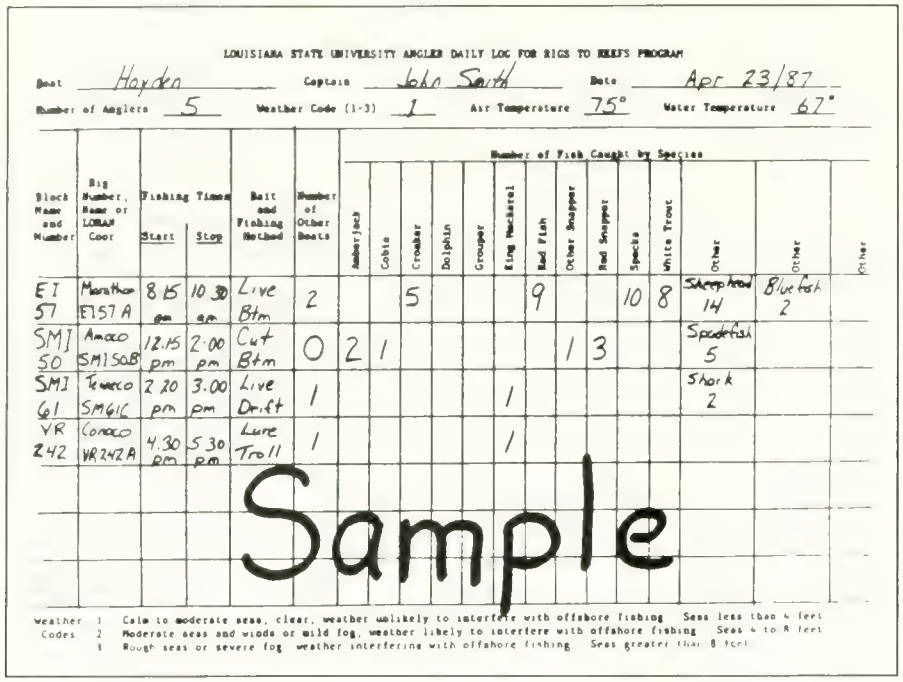

LOUISIANA STATE UNIVERSITY ANGLER DAILY LOG FOR RIGS TO REEFS PROGRAM

Boat: Hayden Captain: John Smith Date: Apr 23/87

Number of Anglers: 5 Weather Code (1-3): 1 Air Temperature: 75° Water Temperature: 67°

Block Name and Number	Rig Number, Name or LORAN Coor	Fishing Time Start	Fishing Time Stop	Bait and Fishing Method	Number of Other Boats	Number of Fish Caught by Species: Amberjack	Cobia	Croaker	Dolphin	Grouper	King Mackerel	Red Fish	Other Snapper	Red Snapper	Speckled	White Trout	Other	Other	Other
EI 57	Marathon EI57A	8:15 am	10:30 am	Live Btm	2			5				9			10	8	Sheepshead 14	Blue fish 2	
SMI 50	Amoco SMI50B	12:15 pm	2:00 pm	Cut Btm	0	2	1						1	3			Spadefish 5		
SMI 61	Texaco SMI61C	2:20 pm	3:00 pm	Live Drift	1						1						Shark 2		
VR 242	Conoco VR242A	4:30 pm	5:30 pm	Lure Troll	1						1								

Sample

Weather Codes: 1 Calm to moderate seas, clear, weather unlikely to interfere with offshore fishing Seas less than 4 feet
2 Moderate seas and winds or mild fog, weather likely to interfere with offshore fishing Seas 4 to 8 feet
3 Rough seas or severe fog weather interfering with offshore fishing Seas greater than 8 feet

Figure 1
Sample page from offshore logbook program.

ing method used by charterboat operators and private vessel anglers. However, Dugas et al. (1979) reported that trolling was the dominant fishing method used by private vessel anglers in Louisiana, with bottom fishing second.

Highest catch rates while trolling off the Louisiana coast by charterboat operators from 1982 to 1985, calculated as number of fish caught/boat hour (CPH), were 9.19 for dolphin in 1982 and 9.04 for Spanish mackerel in 1985 (Brusher et al. 1984, Brusher and Palko 1985, 1987). Bottom-fishing catches off the Louisiana coast by charterboat operators consisted chiefly of Atlantic croaker, red snapper, sand seatrout *C. arenarius*, unidentified seatrout, grey triggerfish *Balistes capricus*, bluefish, and king mackerel, with highest CPH's of 23.45 for sand seatrout and 12.38 for Atlantic croaker in 1984 (Brusher et al. 1984; Brusher and Palko 1985, 1987).

A method by which to test the success or value of an artificial reef and develop a data base on species composition is by tracking the number of fish caught over time, under the assumption that catch per unit effort (CPUE) of the target species is proportional to the abundance of fish. The resultant CPUE can then be used as a measure of relative abundance of fish, and the effects of an artificial reef such as an oil or gas platform can be assessed. For the target species of both the avid recreational angler and researcher, CPUE is a good index of relative abundance (Peterman and Steer 1981, Casselman et al. 1985, Richards and Schnute 1986). Users of such data, however, should be aware that the variability of CPUE estimates can be a problem with any sampling program and can change with different sampling gears. However, Casselman et al. (1985) found that the coefficient of variation of angling catches by experienced, avid, or professional fishermen such as charterboat operators was significantly lower than for other sampling techniques such as trawling, electrofishing, gillnetting, and trapnetting.

The goals of this study were to (1) record and quantify the catch rates and species composition for fish caught by recreational anglers and charterboat operators at or near oil and gas platforms off the Louisiana coast; (2) compare our results with past studies from the northern Gulf of Mexico; and (3) determine the utility of using CPUE estimates of the target species caught near the platforms as an index of their relative abundance.

Materials and methods

Volunteers (120) were solicited to maintain log books from fishing clubs across Louisiana. In addition, 23 charterboat operators listed in National Marine Fisheries Service records, and Coleman (1984) volunteered to maintain logbooks. Study participants were provided with logbooks and program information. Monthly contact was made with study participants to ensure their assistance.

Logbook design was based on the Lake Erie Angler Diary Program (Sztramko 1986) and logbook criteria

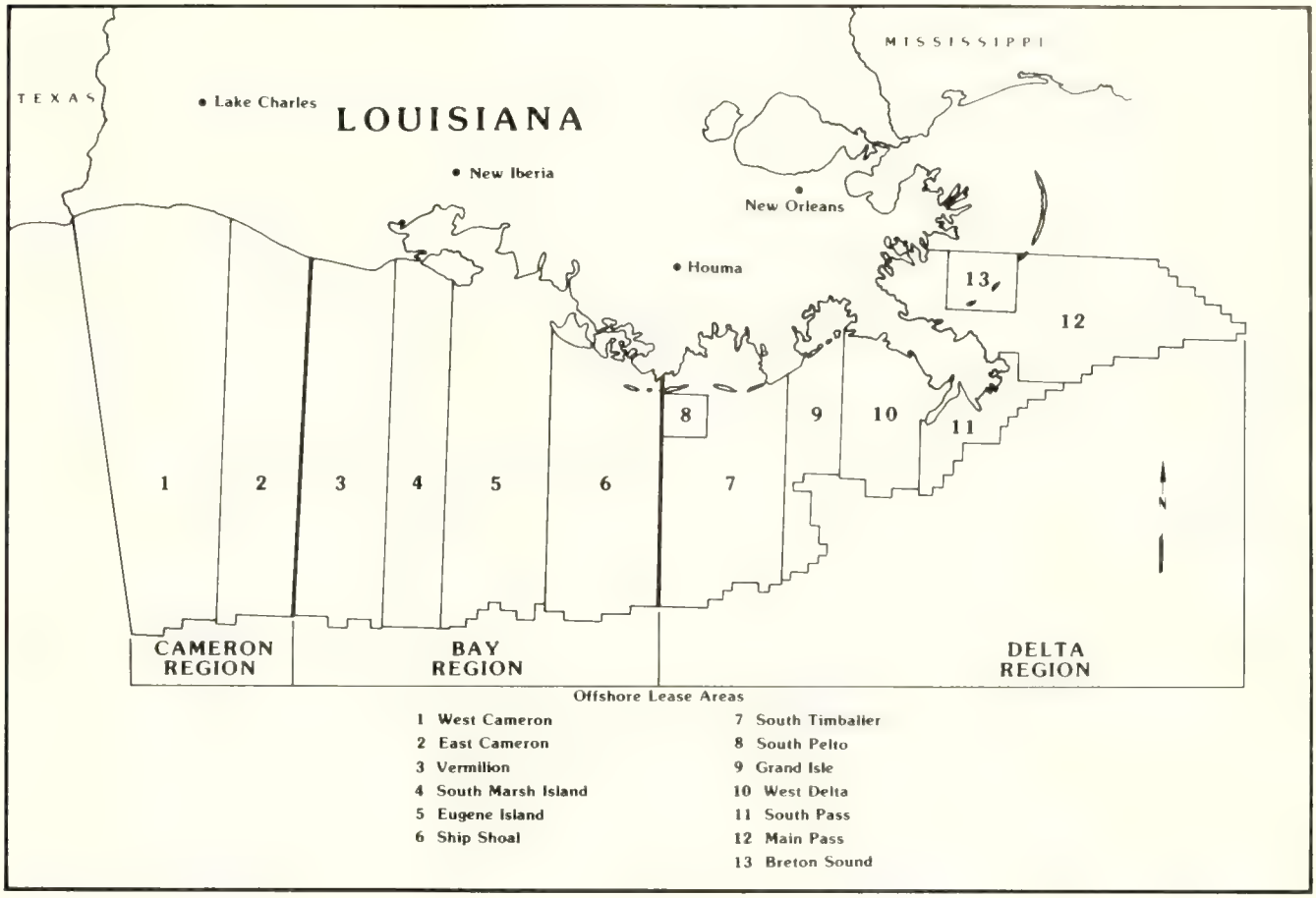

Figure 2
Three regions of the Louisiana offshore study area.

outlined by Demory and Golden (1983). Information entered into the logbooks included date, number of anglers, identity of the oil and gas platform fished, fishing time (not including travel time), fishing method, bait used, and the number of fish caught by species. Participants were asked to complete at least one page of the logbook for each fishing day (Fig. 1). Logbook data were collected from March 1987 to December 1988. Due to the difficulty of identifying certain species of fish such as snapper other than red snapper, groupers, sharks, and silver and sand seatrout, these species were classified as other snapper, groupers, sharks, and silver/sand seatrout, respectively. Other data acquired from study participants included boat length (m), total engine horsepower, and the presence of electronic gear (i.e., LORAN, graph recorders, and echosounders) which aided in the capture of fish. Submerged surface area (m^2) and volume of water enclosed (m^3) by each structure utilized by the participants in 1987 were calculated from schematic diagrams provided by the platform operators.

Fishing effort and CPUE (number of fish caught/angler hour) estimates were separated into two categories: nearshore and offshore fishing. Nearshore fishing around oil and gas platforms was defined as any time at which spotted seatrout were caught, and offshore fishing was defined as trips during which spotted seatrout were not caught. Offshore fishing was further subdivided into bottom fishing (during which time the boat is moored to an oil and gas platform) and trolling. The rationale for the separation of the effort into two categories was due to the segregation of the fish species, as spotted seatrout and red snapper were caught together only 0.7% of the time. Nearshore fishing generally took place in less than 10 m of water where target species were nearshore species such as spotted seatrout, red drum, Spanish mackerel, etc. In contrast, offshore fishing occurred in much deeper water and the target species was usually red snapper; however, a wide range of species were caught with the exception of spotted seatrout. The bait and gear used during the two types of fishing were very different.

Table 1

Descriptive statistics on the number of anglers, man hours, and time spent fishing per oil and gas platform off Louisiana by charterboat operators (CBO) and anglers for inshore fishing and offshore bottom fishing and trolling from logbook records, March 1987–March 1988.

	Time/platform (hrs)				Number of anglers			
	1987		1988		1987		1988	
	Anglers	CBO	Anglers	CBO	Anglers	CBO	Anglers	CBO
Inshore								
N	174	109	62	4	174	109	62	4
Mean	2.8	2.4	2.5	3.6	3.2	3.9	2.8	4.8
SD	2.3	2.3	1.6	2.1	0.8	0.9	0.7	1.0
Offshore bottom								
N	362	578	228	211	362	578	228	211
Mean	2.4	1.3	2.3	1.1	3.7	8.7	3.5	9.6
SD	2.1	1.1	2.1	1.0	2.0	4.6	1.7	3.4
Trolling								
N	130	33	76	14	130	33	76	14
Mean	1.7	2.5	1.4	2.6	3.9	3.5	2.9	4.5
SD	1.8	2.3	1.1	2.3	2.1	1.1	0.9	0.8

While nearshore fishing, light spinning, and bait cast tackle were utilized with natural or artificial baits, offshore fishing tackle generally consisted of heavy boat rods with level wind reels using at least 30-lb test line.

Catch data from various capture methods are usually not distributed normally due to the large number of zero values. Therefore, CPUE was transformed by $\ln(\text{CPUE}+1)$ to approximate the normal distribution of the catch data (Pennington 1983, 1985; Shaw et al. 1985). To compare catch rates of red snapper and spotted seatrout between user groups and years, an ANOVA (SAS 1985) was utilized. A Duncan's multiple range test (SAS 1985) was performed to determine differences in red snapper catches between the three regions of coastal Louisiana (Fig. 2). Based on Univariate Analysis (SAS 1985) of the residuals from ANOVA tests and Duncan's multiple range tests, statistical comparisons could only be made between user groups and years for spotted seatrout and red snapper and among areas and years for red snapper to comply with the assumptions of the statistical tests utilized.

Results

A total of 55 private boat operators and 10 charterboat operators returned usable logbooks in 1987, and 30 private boat operators and 5 charterboat operators in 1988, representing return rates of 45.8% and 43.5% in 1987, and 25.0% and 20.8% in 1988, respectively. Participants fished at 589 different oil and gas platforms 1787 separate times over the study period. Anglers fished at oil and gas platforms on 666 occasions in 1987 and 362 times in 1988. Charterboat operators fished at platforms 530 times in 1987 and 229 times in 1988. In 1987, private vessel and charter operator logbook participants spent a total of 2482 hours fishing, representing 11014 angler hours. During 1988, 1057 vessel hours were spent fishing which accounted for 4780 angler hours of fishing. Charterboat operators carried more fishermen than did the private vessels for all three fishing methods (Table 1).

The most prevalent fishing method for both private boat and charterboat anglers during 1987 and 1988 was offshore bottom fishing. Offshore bottom fishing accounted for 54.5% (1987) and 63.2% (1988) of private vessel fishing trips, and 73.2% (1987) and 92.1% (1988) of charterboat fishing trips. Nearshore fishing and trolling were the next most prevalent fishing methods over the survey period (Table 2).

Study participants most often fished at the large multiwell production platforms, based on the mean submerged surface area and volume of water enclosed by a structure, with charterboat operators fishing at larger platforms than private boat anglers for all three types of fishing (Table 3), although the study participants utilized the available size range of structures from single well caissons to semi-submersible drilling platforms.

Table 2

Boat length, engine horsepower, and frequency of presence of electronic equipment for charterboat and angler logbook participant vessels.

	N	Mean	SD	Min.	Max.
Anglers					
Length (m)	55	7.63	2.18	5.18	18.59
Total engine horsepower	55	298.5	183.7	100.0	1200.0
Charterboats					
Length (m)	10	10.09	2.54	7.62	14.33
Total engine horsepower	10	438.5	154.8	225.0	700.0

	Electronic equipment (%)		
	Echosounders	Graph recorders	LORAN
Anglers	72.7	44.5	67.4
Charterboats	68.9	93.8	93.8

Fishing effort was concentrated in late spring, summer, and early fall for both private boat anglers and charter boat operators. The period from May to September in both 1987 and 1988 constituted over 70% private vessel and charterboat fishing trips (Figs. 3, 4).

Participants caught a total of 44465 fish in 1987 and 16792 fish in 1988 from over 46 different species (Table 4). The five most frequently caught species or species groups in 1987 were (in descending order): red snapper, spotted seatrout, silver/sand seatrout, other snapper, and greater amberjack (Table 4). The five most frequently caught species or species groups in 1988 were (in descending order): red snapper, spotted seatrout, other snapper, silver/sand seatrout, and grey triggerfish (Table 4). These five groups represent 73.4% and 70.4% of the total number of fish caught in 1987 and 1988, respectively (Table 4).

CPUE values of spotted seatrout in 1987 were significantly greater ($P<0.01$) than those of 1988 when all data were pooled by user group (Table 5). When the CPUE estimates of each group were pooled by year, CPUE of charterboat operators for spotted seatrout was significantly greater ($P<0.01$) than that of private vessel anglers. Due to the lack of inshore charterboat participants in 1988, comparisons between user groups and years could not be made. The CPUE estimates of spotted seatrout were approximately one order of magnitude greater than those of other commonly caught fish (i.e., bluefish, red drum, and silver/sand seatrout) while inshore fishing during both sample years (Table 5).

Similarly, offshore bottom-fishing CPUE estimates of red snapper during 1987 and 1988 were approximately one order of magnitude greater than those of other commonly caught fish (i.e., Atlantic croaker, bluefish, greater amberjack, grey triggerfish, grouper, other snapper, and silver/sand seatrout) (Table 5).

Table 3

Descriptive statistics on submerged surface area, volume of water enclosed, and water depth of oil and gas platforms fished by logbook participants while trolling and inshore and offshore bottom fishing off Louisiana, 1987. CBO = charterboat operators.

	Submerged surface area (m^2)		Volume of water enclosed (m^3)		Water depth (m)	
	Anglers	CBO	Anglers	CBO	Anglers	CBO
Inshore						
N	149	96	149	96	149	96
Mean	1500.6	3051.8	6878.7	18421.0	7.9	8.8
Min. value	18.7	46.5	18.1	18.1	2.4	3.1
Max. value	13677.8	13677.8	89174.8	89174.8	37.2	62.5
Trolling						
N	122	31	122	31	122	31
Mean	3359.3	11134.0	25915.7	67522.3	26.7	45.4
Min. value	42.0	720.7	0.0	2103.4	6.7	12.2
Max. value	26319.4	144092.6	316654.4	689118.8	129.5	304.8
Offshore bottom fishing						
N	342	361	342	361	342	361
Mean	3705.2	4275.8	27597.7	32673.6	30.1	38.0
Min. value	24.5	151.8	0.0	0.0	3.1	4.0
Max. value	144092.6	144092.6	689118.8	689118.8	304.8	304.8

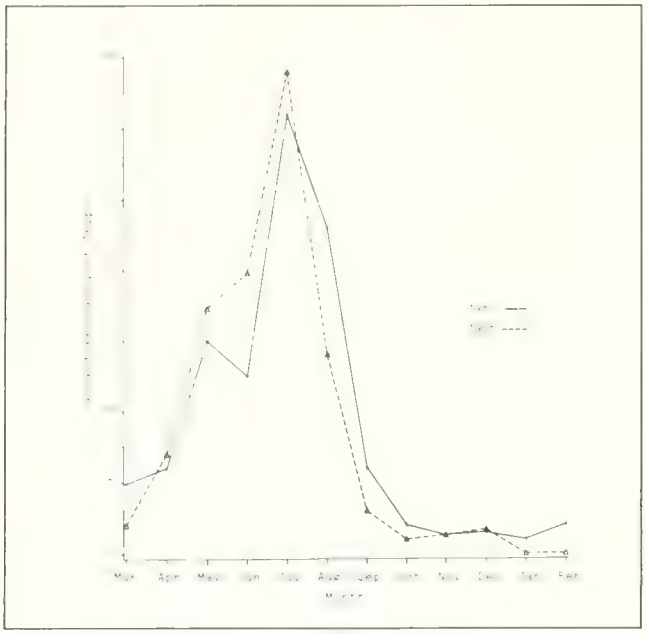

Figure 3
Frequency of offshore fishing trips by month for private vessel angler participants, 1987–88.

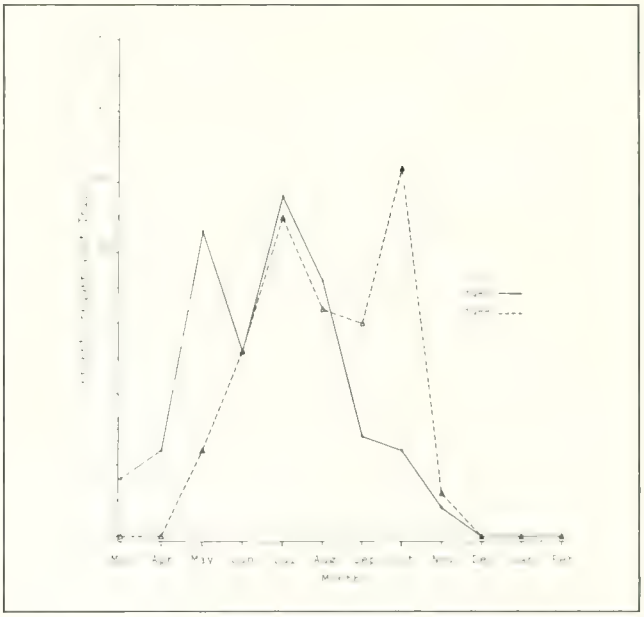

Figure 4
Frequency of offshore fishing trips by month for charterboat operator participants, 1987–88.

Only red snapper were caught often enough to allow statistical comparisons between groups for each year for offshore bottom fishing. Red snapper CPUE of private vessel anglers in 1987 was significantly greater ($P<0.01$) than that of private vessel anglers in 1988 and charterboat operators in 1987 but not significantly greater ($P<0.01$) than that of charterboat operators in 1988.

Offshore trolling CPUE's were not dominated by a single species, nor were they as high as the inshore and offshore bottom fishing CPUE's. Private vessel anglers and charterboat operators most frequently caught blue runner, dolphin, king mackerel, little tunny, and Spanish mackerel while trolling offshore, and the CPUE's of charterboat operators were generally higher, although statistical comparisons were not performed (Table 5).

Private vessel angler and charterboat operator CPUE estimates were pooled for each species to compare CPUE rates between the three regions of coastal Louisiana (Fig. 2) between years. Nearshore CPUE's for all three regions were dominated by spotted seatrout, with the highest CPUE of spotted seatrout found in the Bay region for both 1987 and 1988. The only other striking differences were the CPUE rates of bluefish and red drum which were highest in the Delta region (Table 6). However, due to small sample sizes no statistical comparisons could be performed.

Red snapper CPUE's were the highest in all three regions while offshore bottom fishing. Red snapper CPUE's in the Cameron region during 1987 were significantly greater ($P<0.01$) than those in the Cameron region in 1988; otherwise no significant differences between years or regions for red snapper CPUE were detected (Table 7). Other regional catch differences included much higher CPUE estimates from the Delta region, as opposed to the Cameron and Bay regions, for Atlantic croaker; otherwise no other trends in CPUE were detected between areas or years (Table 7). Due to the large number of zero catches in the species other than red snapper, statistical comparisons could not be performed.

Offshore trolling CPUE estimates from the three regions were not as high or dominated by a single species as were the observed nearshore and offshore bottom-fishing estimates (Table 6). Blue runner, dolphin, little tunny, and Spanish mackerel CPUE's were highest in all three regions. Few trends could be detected between years or regions, as only the CPUE of Spanish mackerel from the Cameron region appeared to be much higher than those of the other species and regions (Table 6), although statistical comparisons could not be made.

Table 4

Composition of catch around oil and gas platforms off Louisiana by logbook participants, 1987–88.

Species/group	1987 No. caught	1987 %	1988 No. caught	1988 %
Atlantic croaker *Micropogonias undulatus*	887	2.0	89	0.5
Atlantic spadefish *Chaetodipterus faber*	23	0.1	110	0.7
Bearded brotula *Brotula barbata*	14	0.0	6	0.0
Black drum *Pogonias cromis*	167	0.4	86	0.5
Blackfin tuna *Thunnus atlanticus*	25	0.1	25	0.1
Bluefish *Pomatomus saltatrix*	1264	2.8	301	1.8
Blue marlin *Makaira nigricans*	4	0.0	1	0.0
Blue runner *Caranx crysos*	279	0.6	256	1.5
Cobia *Rachycentron canadum*	507	1.1	185	1.1
Crevalle jack *Caranx hippos*	63	0.1	26	0.2
Cubbyu *Equetus umbrosus*	5	0.0	—	—
Dolphin *Coryphaena hippurus*	381	0.9	612	3.7
Florida pompano *Trachinotus carolinus*	329	0.7	18	0.1
Flounder *Paralichthys* sp.	8	0.0	12	0.1
Gafftopsail catfish *Bagre marinus*	80	0.2	58	0.3
Great barracuda *Sphyraena barracuda*	93	0.2	19	0.1
Greater amberjack *Seriola dumerili*	1840	4.1	718	4.3
Grey triggerfish *Balistes capriscus*	1221	2.7	990	5.9
Grouper Family: Serranidae	1206	2.7	794	4.7
Grunts *Haemulon* sp.	78	0.2	136	0.8
Hake *Urophycis* sp.	3	0.0	3	0.0
Hardhead catfish *Arius felis*	480	1.1	45	0.3
King mackerel *Scomberomorus cavalla*	543	1.2	201	1.2
Ladyfish *Elops saurus*	29	0.1	3	0.0
Little tunny *Euthynnus alletteratus*	346	0.8	174	1.0
Lookdown *Selene vomer*	9	0.0	28	0.2
Other jacks *Caranx* sp.	54	0.1	9	0.1
Other snapper Family: Lutjanidae	2101	4.7	1355	8.1
Pinfish *Lagodon rhomboides*	127	0.3	74	0.4
Puffer Family: Tetraodontidae	1	0.0	—	—
Rainbow runner *Elagatis bipinnulata*	1	0.0	2	0.0
Rays Family: Dasyatidae	5	0.0	1	0.0
Red drum *Sciaenops ocellatus*	1287	2.9	183	1.1
Red snapper *Lutjanus campechanus*	15385	34.6	6913	41.2
Sharks Order: Selachii	689	1.5	195	1.2
Sheepshead *Archosargus probatocephalus*	39	0.1	25	0.1
Shrimp eel *Ophichthus* sp.	12	0.0	15	0.1
Silver/sand seatrout *Cynoscion* sp.	3663	8.2	974	5.8
Skipjack tuna *Euthynnus pelamis*	624	1.4	258	1.5
Spanish mackerel *Scomberomorus maculatus*	746	1.7	213	1.3
Spotted seatrout *Cynoscion nebulosus*	9688	21.8	1579	9.4
Squirrelfish *Holocentrus* sp.	17	0.0	15	0.1
Tarpon *Megalops atlanticus*	4	0.0	1	0.0
Tripletail *Lobotes surinamensis*	72	0.2	4	0.0
Wahoo *Acanthocybium solandri*	29	0.1	37	0.2
White spotted soapfish *Rypticus maculatus*	9	0.0	—	—
Yellowfin tuna *Thunnus albacares*	5	0.0	4	0.0
Total	44465		16762	

Table 5

Nearshore, offshore trolling, and offshore bottom fishing CPUE of angler and charterboat operator (CBO) logbook participants, 1987–88, near oil and gas platforms off Louisiana.

	1987				1988			
	Anglers		CBO		Anglers		CBO	
Species/group	Mean	(CV)	Mean	(CV)	Mean	(CV)	Mean	(CV)
Nearshore	n = 174		n = 109		n = 64		n = 4	
Bluefish	0.24	(327)	0.03	(491)	0.22	(256)	0.36	(132)
Cobia	0.03	(460)	0.01	(550)	-		0.01	(200)
Hardhead catfish	0.03	(593)	–	–	0.05	(526)	–	–
Red drum	0.16	(330)	0.33	(327)	0.18	(189)	0.56	(98)
Sharks	0.04	(509)	–	–	0.02	(445)	–	–
Silver/sand seatrout	0.55	(374)	0.14	(348)	0.63	(288)	1.40	(200)
Spanish mackerel	0.03	(980)	–	–	0.02	(547)	–	–
Spotted seatrout	3.94	(131)	5.48	(74)	3.33	(138)	0.83	(158)
Offshore bottom fishing	n = 362		n = 578		n = 222		n = 211	
Atlantic croaker	0.17	(631)	0.08	(330)	0.11	(452)	0.01	(698)
Bluefish	0.30	(510)	0.11	(429)	0.11	(608)	0.01	(549)
Blue runner	0.11	(1129)	0.02	(1061)	0.09	(546)	-	
Cobia	0.08	(360)	0.06	(323)	0.07	(342)	0.04	(258)
Dolphin	0.05	(916)	0.02	(1207)	0.01	(1051)	0.01	(1087)
Greater amberjack	0.30	(391)	0.25	(272)	0.24	(484)	0.19	(264)
Grey triggerfish	0.28	(311)	0.14	(329)	0.39	(289)	0.19	(160)
Grouper	0.23	(282)	0.22	(255)	0.21	(265)	0.30	(158)
Hardhead catfish	0.11	(641)	0.06	(705)	0.01	(1490)	0.01	(908)
King mackerel	0.04	(364)	0.05	(335)	0.03	(626)	0.04	(299)
Other snapper	0.19	(377)	0.37	(245)	0.05	(321)	0.47	(183)
Red drum	0.11	(385)	0.07	(762)	0.06	(462)	–	–
Red snapper	2.83	(171)	2.11	(155)	2.12	(248)	2.53	(148)
Sharks	0.06	(556)	0.12	(431)	0.04	(608)	0.05	(304)
Silver/sand seatrout	0.82	(388)	0.32	(298)	0.30	(256)	0.01	(693)
Spanish mackerel	0.08	(615)	0.03	(1013)	0.02	(887)	–	–
Offshore trolling	n = 130		n = 33		n = 76		n = 14	
Blue runner	0.34	(308)	0.03	(441)	1.02	(229)	0.03	(374)
Cobia	0.02	(397)	0.08	(266)	0.01	(699)	0.02	(296)
Crevalle jack	0.07	(398)	0.10	(446)	0.05	(387)	–	–
Dolphin	0.26	(372)	0.71	(236)	0.25	(502)	1.23	(167)
Greater amberjack	0.12	(598)	0.09	(377)	0.09	(356)	–	–
King mackerel	0.11	(623)	0.62	(151)	0.25	(232)	0.17	(171)
Little tunny	0.43	(222)	0.85	(209)	0.78	(162)	0.21	(241)
Other jacks	0.07	(623)	0.08	(400)	0.02	(872)	–	
Spanish mackerel	0.51	(271)	0.64	(222)	0.84	(227)	0.42	(288)

Discussion

Private vessel anglers and charterboat operators caught a total of 61227 fish representing over 46 different species. The fishing habits and boat characteristics of study participants were as expected. Peak fishing by private vessel anglers and charterboat operators occurred during the summer which agreed with past studies by Ditton and Auyong (1984) and Stanley and Wilson (1989). During other times of the year, cold fronts and other severe forms of weather make fishing off the coast of Louisiana nearly impossible or at least uncomfortable. Based on number of trips, the most prevalent fishing method was offshore bottom fishing, with nearshore and offshore trolling the next most popular methods for the study participants.

Private vessel anglers and charterboat operators utilized the entire range of platform sizes and operational types off the coast of Louisiana. Single well structures, steel template platforms, and mobile semisubmersible drilling platforms were commonly fished, although certain trends in platform size utilization and fishing method were apparent. Nearshore anglers most often fished at the small, single well structures

Table 6

Nearshore and offshore trolling CPUE of logbook participants around oil and gas platforms in the Delta, Bay, and Cameron Regions off Louisiana, 1987–88.

	Delta		Bay		Cameron	
	1987	1988	1987	1988	1987	1988
Species/group	Mean (CV)	Mean (CV)	Mean (CV)	Mean (CV)	Mean (CV)	Mean (CV)
Nearshore	$n = 48$	$n = 8$	$n = 196$	$n = 46$	$n = 37$	$n = 12$
Bluefish	0.68 (197)	1.28 (64)	0.04 (537)	0.02 (678)	0.14 (324)	0.22 (234)
Cobia	0.06 (259)	0.03 (144)	0.01 (947)	— —	0.02 (370)	— —
Hardhead catfish	— —	— —	0.03 (606)	0.07 (444)	— —	— —
Red drum	0.99 (169)	0.80 (49)	0.02 (660)	0.11 (249)	0.39 (258)	0.07 (186)
Sharks	0.01 (495)	0.03 (494)	0.03 (632)	0.03 (439)	0.05 498)	— —
Silver/sand seatrout	0.25 (326)	0.08 (282)	0.38 (444)	0.85 (249)	0.53 (226)	0.55 (293)
Spanish mackerel	0.09 (557)	— —	0.02 (608)	0.01 (475)	0.02 (608)	0.07 (346)
Spotted seatrout	1.73 (125)	0.48 (70)	5.70 (87)	4.28 (119)	2.02 (97)	1.29 (83)
Offshore trolling	$n = 78$	$n = 50$	$n = 23$	$n = 13$	$n = 63$	$n = 27$
Bluerunner	0.46 (260)	0.71 (230)	0.20 (425)	1.06 (234)	0.09 (441)	1.06 (269)
Cobia	0.04 (372)	0.02 (592)	0.03 (303)		0.03 (369)	0.01 (388)
Crevalle jack	0.01 (590)	— —	0.07 (268)	0.07 (361)	0.15 (311)	0.10 (263)
Dolphin	0.20 (276)	0.48 (363)	0.68 (298)	0.15 (177)	0.40 (312)	0.39 (298)
Greater amberjack	0.05 (630)	— —	0.14 (315)	0.27 (158)	0.18 (509)	0.12 (350)
King mackerel	0.04 (455)	0.05 (506)	0.07 (209)	0.29 (165)	0.49 (157)	0.55 (140)
Little tunny	0.69 (205)	0.73 (173)	0.14 (215)	0.50 (174)	0.43 (199)	0.72 (174)
Other jacks	0.08 (625)	0.03 (707)	0.14 (381)	— —	0.05 (498)	— —
Spanish mackerel	0.25 (363)	0.24 (262)	0.28 (270)	0.46 (302)	1.06 (196)	1.91 (145)

Table 7

Offshore bottom fishing CPUE of logbook participants around oil and gas platforms in the Delta, Bay, and Cameron Regions off Louisiana, 1987–88.

	Delta		Bay		Cameron	
	1987	1988	1987	1988	1987	1988
Species/group	Mean (CV)	Mean (CV)	Mean (CV)	Mean (CV)	Mean (CV)	Mean (CV)
	$n = 627$	$n = 280$	$n = 196$	$n = 77$	$n = 153$	$n = 75$
Atlantic croaker	0.16 (518)	0.10 (485)	0.02 (694)	— —	0.04 (393)	— —
Bluefish	0.23 (592)	0.02 (539)	0.11 (422)	0.25 (437)	0.08 (689)	0.02 (672)
Cobia	0.05 (367)	0.05 (362)	0.14 (310)	0.08 (282)	0.08 (242)	0.05 (273)
Greater amberjack	0.30 (331)	0.11 (487)	0.18 (325)	0.15 (235)	0.25 (224)	0.65 (275)
Grey triggerfish	0.26 (287)	0.25 (217)	0.07 (571)	0.50 (288)	0.09 (386)	0.23 (391)
Grouper	0.26 (238)	0.30 (183)	0.16 (416)	0.20 (283)	0.15 (277)	0.15 (230)
King mackerel	0.02 (449)	0.03 (384)	0.07 (198)	0.02 (330)	0.14 (224)	0.07 (439)
Other snapper	0.40 (240)	0.56 (217)	0.13 (508)	0.55 (329)	0.07 (336)	0.14 (542)
Red drum	0.10 (524)	0.02 (876)	0.09 (633)	0.02 (445)	0.05 (338)	0.08 (356)
Red snapper*	2.33 (187)^{ab}	2.27 (162)^{ab}	2.62 (124)^{ab}	2.72 (247)^{ab}	2.85 (132)^{a}	2.19 (237)^{b}
Sharks	0.11 (421)	0.05 (428)	0.03 (379)	0.04 (591)	0.08 (596)	0.02 (301)
Silver/sand seatrout	0.68 (369)	0.20 (328)	0.17 (383)	0.15 (363)	0.12 (460)	0.02 (699)
Spanish mackerel	0.02 (1153)	0.01 (1471)	0.12 (536)	0.01 (560)	0.12 (498)	0.02 (442)

* Means with the same letter are not significantly different at the 1% level.

in shallow water, while offshore bottom fishing and trolling anglers fished much larger steel template platforms in deep water. These results provide evidence that participants were maximizing their catch potential, as Stanley (1989) found highest abundances of spotted seatrout near small platforms in shallow water, while highest abundances of red snapper and related species were found near large platforms (sub-

merged surface area 8000–14000 m^2) in 70–100 m of water.

Charterboat operators had larger vessels than private vessel anglers due to the business nature of their fishing and larger party size. Using larger vessels, they were able to fish in deeper waters farther offshore than private vessel anglers for both offshore bottom fishing and trolling. Charterboat operators also fished in deeper water while fishing nearshore; however, this is probably not a direct function of boat size, but of past success and preference.

A high diversity of fish exist around the oil and gas platforms as evidenced by the reported catch of over 46 different species. The types of fish caught ranged from relatively common and highly desirable species such as spotted seatrout, red snapper, tarpon, blue marlin, king mackerel, and yellowfin tuna to rather rare fishes such as hake, bearded brotula, and squirrel fish. However, catches by angling are selective and biased towards larger, carnivorous individuals due to the gear utilized (Grimes et al. 1982). Therefore, species not susceptible to angling were not represented.

Comparison of CPUE estimates between this study and logbook programs from other parts of North America revealed CPUE estimates were generally much higher off the Louisiana coast than from other studies. CPUE estimates from Sztramko (1986) for Lake Erie, Ontario, private vessel anglers and charterboat operators were approximately 0.15 for the target species of smallmouth bass *Micropterus dolomieui* and coho salmon *Oncorhynchus kisutch*, while Casselman et al. (1985) reported CPUE estimates of 0.30 for northern pike *Esox lucius* by sportfishing guides on the St. Lawrence River, Ontario. Only CPUE estimates from logbooks maintained by commercial fishermen trolling for Pacific salmon (Jordan and Carter 1987) were as high as CPUE estimates from this study.

Catch rates in this study, presented as number of fish per angler per hour, are not directly or statistically comparable with those reported by Brusher et al. (1984), Brusher and Palko (1985, 1987), and other earlier studies from the Gulf of Mexico because they used number of fish caught per boat per hour (CPH) as a unit of relative abundance. Since the number of anglers on a sportfishing vessel can be highly variable, catch per vessel hour may also be highly variable. By calculating the number of fish caught per angler hour, catch is broken down to its most standard unit, assuming the skill level of anglers is equal, thus eliminating this source of variance.

CPH rates by bottom fishing and trolling from this and other studies off the Louisiana coast were much higher than in other regions of the Gulf of Mexico and the southeast Atlantic. However, when mean number of anglers was multiplied by CPUE for charterboat operators from this study and compared with Brusher et al. (1984) and Brusher and Palko (1985, 1987), similar catch rates were noted for the Louisiana coast.

Comparison of the catch rates and composition of trolling from this study and others revealed few differences. Brusher et al. (1984) and Brusher and Palko (1987) found trolling catches of charterboat operators off Louisiana were primarily comprised of dolphin, Spanish mackerel, red drum, little tunny, king mackerel, and blue runner. We found little change in this trend with the exception of red drum. Based on our results, red drum do not appear to be associated with oil and gas structures. Other logbook programs off the Louisiana coast did not distinguish between areas fished (near oil and gas platforms or otherwise) (Dugas et al. 1979), and consequently red drum catches may have been high in areas not covered by our logbook program, which may explain their absence from our results.

When catch rates and composition of our study were compared with those of other logbook programs and a creel census for offshore bottom fishing, major differences in catch composition were noted. Past studies conducted during 1978 by Dugas et al. (1979), in 1982 by Brusher et al. (1984), and during 1984–85 by Brusher and Palko (1987), found that Atlantic croaker and silver/sand seatrout dominated catches of charterboat operators while we found that red snapper catch rates were often an order of magnitude greater than for all other species caught. Since many of the same charterboat operators were utilized by both ours and earlier studies, these differences may provide evidence that there has been a shift in the species abundance near oil and gas platforms in offshore waters with little or no change in the composition of the structure (i.e., the number of oil and gas platforms) off the Louisiana coast. Comparison of our nearshore catches around oil and gas platforms with those of creel surveys of Texas bay charterboat operators from 1978 to 1979 (McEachron and Matlock 1983) showed that spotted seatrout dominated the catch rate and composition of nearshore Texas fishermen as they did in Louisiana, although spotted seatrout catches off Louisiana were much higher than for Texas sport fishermen.

Overall CPUE's of all species between private vessel anglers and charterboat operators were very similar; however, charterboat operator CPUE was generally less variable. Few trends were identified from comparisons between years or user groups. Only for spotted seatrout was charterboat operator CPUE consistently higher than private vessel angler CPUE; otherwise few differences were noted between the two groups. The similarity of the CPUE's indicated that the anglers participating in the logbook program were avid,

knowledgeable fishermen who were as skilled as the professional charterboat operators.

The CPUE of the study participants was probably much higher than that for average offshore saltwater fishermen in Louisiana. Since charterboat operators are professional fishermen who make their living by catching fish, and the private vessel anglers participating in the program were equally as skilled, the catch rates by these groups do not reflect average catches. Both groups have a higher success rate than do casual fishermen who rarely catch fish due to improper techniques and do not target their effort (Casselman et al. 1985). Consequently, the CPUE's presented are not applicable to all fishermen, only to skilled, dedicated, amateur anglers and charterboat operators.

Spotted seatrout and red snapper were the target species of private vessel anglers and charterboat operators, as indicated by their domination of respective CPUE estimates for nearshore and offshore bottom fishing and based on past research from a saltwater recreational angling survey (Stanley and Wilson 1989). Casselman et al. (1985) reported that the CPUE of avid recreational fishermen can be used as an index of relative abundance, and if data are collected over a long period of time, changes in CPUE can reflect fluctuations in the populations of the target species. Offshore trolling CPUE was not dominated by a single species, indicating that fishermen were not targeting their effort for any particular species; therefore, CPUE estimates while trolling would not reflect changes in abundance to the same extent as nearshore and offshore bottom-fishing CPUE estimates.

Conclusions

The catch rates of private vessel anglers and charterboat operators around oil and gas platforms in the northern Gulf of Mexico were high, with their effort targeted towards red snapper while offshore bottom fishing, and spotted seatrout while nearshore fishing. Catch rates while trolling were more uniform and not dominated by any one species. Catch rates between the user groups and across the regions were similar, although some minor differences were detected.

Based on comparisons of catch rates and composition between our results and past studies, a shift in the abundance of certain species has occurred near oil and gas platforms off the Louisiana coast. Studies from 1978 to 1985 found Atlantic croaker and silver/sand seatrout constituted the largest portion of the catch and had the highest catch rates, while we found that red snapper dominated the catch statistics while offshore bottom fishing. Little change in the patterns of species abundance appears to have occurred for species targeted while offshore trolling and nearshore fishing around oil and gas platforms, based on comparisons with earlier studies.

The physical construction of oil and gas platforms precludes the sampling of the associated sportfish populations using traditional methods (e.g., gillnets, trawls). The success of this logbook program indicates that the collection of CPUE data over long periods of time may be an effective technique of monitoring fish populations associated with the platforms. Although the data supplied by the logbooks is an index of relative abundance of fish susceptible to angling and is biased towards larger individuals, it provides a valuable source of data which is otherwise difficult to obtain.

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Survival of King and Tanner Crabs Captured by Commercial Sole Trawls

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Abstract.–King crabs *Paralithodes camtschaticus* and Tanner crabs *Chionoecetes bairdi* captured incidentally by Bering Sea trawlers were examined for immediate mortality, vitality, and injuries resulting from trawl capture. A number were held aboard ship for 2 days in seawater to determine delayed mortality. Overall survival, including immediate and delayed effects, was 21% (±2.0%) for king crabs and 22% (±3.6%) for Tanner crabs. Immediate mortality of king crabs decreased significantly with shell age, and increased significantly with time in captivity prior to assessment, from 0% at 3 hours to 100% at 17 hours. Vitality, an index of spontaneous activity level, was a better predictor of delayed mortality than was the presence/absence of injuries. The effect of leg and body injuries on mortality of king crabs was similar, but injuries to leg segments proximal to the plane of autotomy resulted in higher mortality than injuries distal to the autotomy plane, or autotomization alone.

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Capture and subsequent mortality of nontarget (bycatch) species is a major problem facing managers of multispecies fisheries. In the U.S. eastern Bering Sea (EBS), joint-venture (JV) trawl fisheries targeting on yellowfin sole *Limanda aspera*, rock sole *Lepidopsetta bilineata*, and Pacific cod *Gadus macrocephalus*, routinely catch red king crabs *Paralithodes camtschaticus* and Tanner crabs *Chionoecetes bairdi* and *C. opilio*. In 1988, 88000 red king crabs, 751000 *C. bairdi*, and 2.4 million *C. opilio* were captured in 1.30 million metric tons (t) of groundfish by JV fishing vessels, representing catch rates of 0.07, 0.58, and 1.84 crabs/t, respectively (Berger and Weikart 1989). Additional quantities of these crab species were also captured by domestic fishermen, but their numbers are unknown due to the absence of an effective domestic fishery observer program. All three species of crab are designated as 'Prohibited species' by the North Pacific Fishery Management Council (NPFMC), and must be returned to sea. Nonetheless, mortality of incidentally caught crab is considered to be 100%, and represents losses from the directed crab fisheries.

Due to concerns expressed by crab fishermen about the effects of bycatch on crab populations, a portion of the EBS was closed to trawling by the NPFMC in 1986 to protect king crabs, and has remained closed to date. In addition, maximum catch rates (crabs/t) and caps on total crab catch have been defined for particular regions of the EBS. Somerton and June (1984) attempted to quantify the relative costs to the crab fishery and benefits to the trawl fishery from conducting trawl fisheries on crab grounds, in order to designate those areas with negative relative costs as a king crab conservation zone, but their recommendations were never implemented per se.

The establishment of caps and maximum allowable catch rates was predicated on the assumption that all crabs captured incidentally to trawl fisheries subsequently die. However, this is not necessarily the case. In August of 1988, the opportunity arose to conduct an experiment to determine the survival rate of crab caught incidentally by the JV trawl fishery. This was conducted in conjunction with a study to determine the effectiveness of experimental nets designed to reduce the bycatch of crab. The goals of the study were to determine immediate and delayed survival and mortality of crabs, and the effects on survival of injuries, size and shell age of crabs, processing time, and gear (trawl) type.

Materials and methods

Definitions

The term survival (S), as used in this report, means the proportion of a given group of crabs which was alive at a specified time. Mortality (M) is the complement of this value, i.e., 1 – S. In this investigation, survival was treated as a two-step process; immediate survival (ISURV) or mortality (IMORT) is the proportion determined to be alive or dead, respectively, when the crabs were first

examined and measured. Delayed survival (DSURV) or mortality (DMORT) is that portion alive or dead after crabs were held in seawater for a specified time period.

Sampling technique

An experiment was conducted during the period 12 August—12 September 1987 to compare catch rates between standard Bering Sea joint venture commercial sole trawls and two experimental nets designed to reduce the bycatch of crabs (Highliners Association 1988). Although the results of that experiment are not discussed in this report, the experimental design will be briefly described in order to facilitate understanding of the survival experiment. During the study, five Bering Sea combination trawlers made 307 tows within an area of the EBS between lat. 57° and 58°N, and between long. 162° and 163°W. Tows ranged from 1 to 6.4 hours in length and averaged 20 metric tons (t) of fish. Target species were yellowfin sole *Limanda aspera*, rock sole *Lepidopsetta bilineata*, and Pacific cod *Gadus macrocephalus*. One vessel fished continuously with a previously used 'Standard' trawl (STD). The four other vessels rotated four trawls between them including two new and unused standard trawls, referred to as 'Control 1' (C1) and 'Control 2' (C2), and two experimental trawls. One of the experimental trawls, referred to as the 'Panel' (PAN) trawl, had the front portion of the bottom panel removed and replaced with longitudinal lines, such that crabs could fall out the bottom of the net after passing over the footrope. The second experimental trawl, referred to as the 'Chute' (CHU) trawl, had a webbed funnel-shaped chute sewn into the lower half of the net at the junction between the belly and intermediate section, such that anything entering the mouth of the chute would exit the bottom of the net. During the experiment, codends from each trawl were delivered to the USSR MV *Sulak* at 2–3 hour intervals, where they were sampled by biologists before processing.

Once onboard the *Sulak*, codends were dumped, and all crabs were recovered by sorting through the entire catch. The first 21 tows were dumped on deck and crabs sorted there. The remainder of the tows were dumped directly into storage bunkers, and crabs were recovered from the processing line conveyor in the factory, as the fish were processed. All crabs were sorted by species (and usually by sex), placed into plastic baskets (~25 kg capacity), and weighed. Because of logistic constraints, higher priority was assigned to collecting data on king crabs than on Tanner crabs. Total numbers were determined either by direct counting, or by counting and weighing a subsample. When subsampling occurred, each crab was assigned a sampling factor equal to the proportion of the total number of crabs in the tow represented by the subsample. Crabs were then treated in one of four ways:

(A) Measured crabs Up to 150–200 crabs of each species from each haul were measured to the nearest 1.0 mm with steel vernier calipers. Subsampling occurred when >200 of either species were captured. King crabs were measured from the rear of the right eyesocket to the midpoint of the rear margin of the carapace (carapace length, CL). Tanner crabs were measured across the widest portion of the carapace, including spines (carapace width, CW). Shell conditions were coded as 1 = molting, or recently molted with a soft or flexible shell; 2 = hard shelled but molted within recent year, without epifauna or scratches; 3 = oldshell or skipmolt, with scratches, epifauna, scars, or damaged dactyls.

(B) Vitality coding For most hauls, all measured crabs were also given a vitality code on a 3-point scale: (1) alive and active, i.e., exhibiting spontaneous vigorous movement of appendages and attempting to escape or pinch the examiner; (2) moribund (alive but inactive), i.e., exhibiting only slow weak movements, or only in response to prodding; and (3) dead. In practice, death was not easy to determine, as some crabs which initially appeared dead would exhibit spontaneous movements after examination. After the first few tows, a criterion was developed which consisted of (a) looking for spontaneous movement of appendages, (b) lacking that, attempting to stimulate movement by moving and bending appendages, followed by (c) flicking the mouthparts with a finger three times at 5–10 second intervals. The minimum requirement for a vitality code of 2 was any spontaneous movement of the antennules or any other appendage. These criteria were tested by placing 30 crabs which were classified as dead into the live tanks; none recovered. Presence or absence of injuries was not a criterion used in this coding procedure.

(C) Injury assessment Approximately 30–40 king crabs per tow (usually the first basket examined of each sex) and occasional Tanner crab were examined for injuries. Since there was considerable shuffling and repositioning of crabs and baskets during the weighing and subsampling process, this was assumed to be a random sample, and represents a subset of the crabs examined for vitality in step B above. Examination entailed a visual scan of the carapace, sternum, abdomen, and each leg in turn. Bodily injuries were recorded as present or absent. Leg injuries were categorized as being distal to the autotomy or breakage plane, proximal to the breakage plane, or recent autotomy, distinguished by the presence of a clear membrane with

no discoloration or scarring. The number of legs with each of these three types of injuries was recorded.

(D) Survival or delayed mortality A subset of the injury-assessed crabs (Step C) was placed into one of four tanks of flowing seawater, $\sim 1.0 \times 1.0 \times 0.7$ m, and held for 48 hours, after which they were reexamined for delayed mortality, using the same procedures outlined above for vitality. The subset usually consisted of all crabs coded for injures from one haul per day, although towards the end of the experiment several hauls per day were treated in this manner. Crabs which were determined to be dead before placement into the tanks were retained for at least 6 hours for confirmation before removal.

Crab processing time was recorded for each tow as the interval between the arrival of the codend on deck and the time the crabs were examined and measured. Although examination usually required anywhere from 0.5 to 1.5 hours for an entire sample, the midpoint of that period was used as the mean endpoint of processing time for all crabs in a haul. Towing time, i.e., the difference between the time the net was determined to be on bottom and the time haulback started, was obtained from each catcher vessel and divided by 2, in order to approximate the average time each crab spent in the net before delivery to the *Sulak*. Total capturing and processing time (CAPTIME) was calculated as the sum of (towing time)/2 and processing time.

Total weight of the catch in each haul was estimated by measuring the height and width of the codend at several intervals along its length, and calculating the volume based on the shape of an oblate cylinder, with density determined by weighing a known volume of fish.

Data analysis

In order to improve the precision of the survival estimates, overall survival was calculated for each species in a stratified manner (Cochran 1963). Vitality codes were used as strata because they provided additional information on the probability of survival, i.e., crabs coded as alive and active were deemed more likely to survive than crabs coded as moribund. For immediate survival estimates only, each crab was weighted by the sampling factor for the tow from which it originated. Estimates of delayed mortality were not weighted, because subsampling was accounted for at the level of immediate mortality. The formulae used were:

$$S_{st} = 1/N \sum N_v p_v \quad (1)$$

and

$$V(S_{st}) = 1/N^2 \sum N_v (N_v - n_v) p_v q_v / (n_v - 1) \quad (2)$$

where S_{st} = stratified estimate of population survival rate,
$V(S_{st})$ = variance of stratified estimate,
N_v = number of crabs in stratum (vitality group) v,
n_v = number sampled from stratum v (placed in live tanks),
p_v = proportion of subsample surviving in live tanks,
$q_v = 1 - p_v$,
N = weighted total number of crabs given vitality codes.

The effect of CAPTIME on immediate mortality was determined by fitting the data to a logistic curve. Crabs were grouped into hourly intervals of CAPTIME (as described above), and mortality data (weighted by sampling factors) for each interval were fitted using an iterative procedure (FSAS FISHPARM, Saila et al. 1988). The equation fitted was:

$$M = 1/\{1 + \exp(-r[X - X_{50}])\} \quad (3)$$

where M is expected mortality and $0 \leq M \leq 1$, X is the value of the predictor variable (CAPTIME) in hours, and r and X_{50} are parameters of the equation, the latter representing the time required for 50% mortality to occur. Both king and Tanner crabs were treated separately. Delayed and overall survival were not fitted because there were too few observations. The effect of total catch weight on immediate survival was also determined in the same manner, with crab data grouped by catch weight intervals of 1.0 t.

To determine the effect of size, crabs were grouped by 15-mm intervals of CL (king crab) or CW (Tanner crab). For king crabs, immediate, delayed, and overall mortality were calculated for each size group. Only immediate mortality was calculated for each size group of Tanner crabs, due to limited data. Immediate mortality was also determined for each gear type, by species.

Procedures used by National Marine Fisheries Service (NMFS) observers aboard fishing vessels to code crab vitality differ from those used in this study. In this study, vitality codes were based on activity level of crabs regardless of injuries, and injuries were coded separately, whereas the NMFS observer method is to assign a vitality code of 1 for crabs which are active and uninjured, and a vitality code of 2 for crabs which are either inactive or injured. Contingency table and loglinear analysis was performed in order to assess the difference between these two methods and determine which provided the best estimate of delayed mortality, and to determine the relative contribution of vitality and injuries to subsequent delayed mortality. Three

sets of 2×2 contingency tables were analyzed using the X^2 statistic, which is approximately distributed as the chi-squared distribution, and which is equivalent to the G-statistic for 2×2 contingency tables (Sokal and Rohlf 1981). Only two-way interactions can be identified with this procedure, so factors tested were vitality vs. injuries, vitality vs. mortality, and injuries vs. mortality. The null hypothesis tested was that effects of both factors were independent of each other, i.e., that no interactions occurred.

Loglinear analysis was accomplished to determine the odds of mortality associated with vitality level and injury presence. The SPSS LOGLINEAR (SPSS Inc. 1986) procedure was used to fit a logit model, in which one dichotomous factor—delayed mortality (DMORT)—was designated as a dependent variable, and the remaining factors—vitality (VIT) and injuries (INJ)—were the independent variables. Only live crabs were used, i.e., those with vitality codes of 1 or 2; injury codes were 1 (uninjured) or 2 (injured), and DMORT was coded as 1 (survived) or 2 (died). The data fit by the model were the log-transformed survival odds (ratio of survivors to mortalities), often referred to as logits, in each category of the independent variables (vitality and injuries):

$$\text{Logits} = \ln(\text{ODDS}) = \ln(f_s/f_m) \quad (4)$$

where f_s and f_m are the observed frequencies of survivors and mortalities, respectively. The logit model used for fitting entails expressing the logits as a linear model of several parameters:

$$\ln(f_s/f_m) = 2(l_D + l_{D*V} + l_{D*I}) \quad (5)$$

where f_s, f_m = observed number of survivors or mortalities,
l_D = parameter estimate for DMORT (mean odds of mortality),
l_{D*V} = parameter for interaction of DMORT and vitality,
l_{D*I} = parameter for interaction of DMORT and injuries.

The proportion of crabs in any cell of the model which survive is related to the survival odds by the formula:

$$S = (1 + \text{ODDS}^{-1})^{-1} \quad (6)$$

This model assumes that a mean level of mortality would occur regardless of other factors, and that each confounding factor increases mortality in a logarithmic fashion, or that the overall odds of survival are the sum of the logs of the parameter estimates for each contributing factor. In this model, there are two alternative outcomes for each category, which have equal and opposite parameter values which must sum to 0. For instance, parameter 1 represents the alternatives of survival vs. mortality; parameter 2 represents the positive contribution of a 'good' vitality code of 1 vs. the negative influence of a 'poor' vitality code of 2; parameter 3 is similar to parameter 2 with regard to the influence of the presence vs. absence of injuries. Since the model represents the log of a ratio, the effect attributable to any single factor is calculated as the difference between parameter estimates for alternative outcomes, e.g., the total effect of DMORT is $l_D - (-l_D)$, or $2(l_D)$. Thus the entire equation is multiplied by a factor of 2.

Table 1
Number of crabs sampled during survival study. Each category below "Measured" is a subset of the one above it.

Disposition	King crab	Tanner crab
Measured	18804	31318
Vitality coded	6113	4645
Injuries coded	2835	518
Survival coded	617	74

Each cell of the contingency table was coded as 1 or 2 for each factor. Crabs which were active, uninjured, and survived, for instance, were coded as 1,1,1. Similarly, crabs which were inactive, injured, and died were coded 2,2,2. The parameter value for the effect of vitality on mortality (l_{D*V} in the above model) was calculated for cases with equal codes for DMORT and VIT (i.e., both equal to 1 or both equal to 2); the parameter estimate for cases with unequal codes was equal but opposite in sign. Individual parameters were converted to odds by calculating the antilog. Odds for any combination of categories is equivalent to the product of antilogs of parameters (or the sum of all parameters times 2) for all factors in the model.

The interaction of immediate mortality (IMORT) with body injuries (BODY) and leg injuries (LEGS) was investigated in an identical manner. Values of the variables BODY and LEGS were set to 1 if no injury was present, or 2 if an injury was present.

Contingency table analysis using the X^2 statistic was performed to test the null hypothesis that immediate mortality was independent of three types of leg injury, defined as autotomization, injuries distal to the autotomy or breakage plane, and injuries proximal to the breakage plane. The X^2 statistic was also used to test the independence of immediate and delayed mortality from shell condition, and the number of legs with injuries.

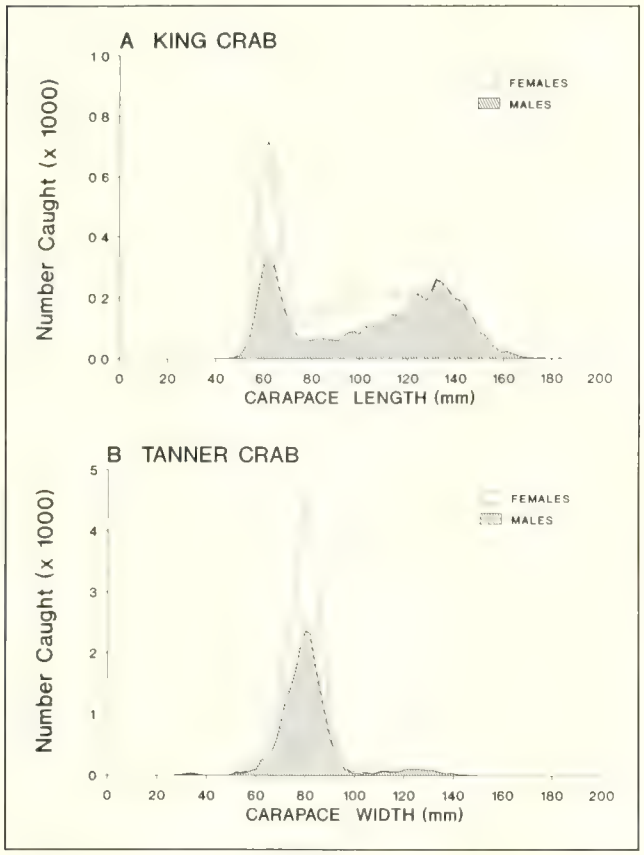

Figure 1

Size frequency of crabs caught during the experiment, shown as a moving average of three 1-mm intervals. Numbers are expanded from number measured by sampling factors. Sexes are stacked.

Results

Over 6200 t of fish were sorted through during the study, and over 50000 crabs were recovered and measured (Table 1), the majority being Tanner crabs (which shall be used herein to refer only to the species *Chionoecetes bairdi*), and the remainder mostly king crabs *Paralithodes camtschaticus*. A few *C. opilio* were encountered but are not discussed here. Vitality was coded on over 10750 crabs, representing 23985 total crabs after expansion by subsampling factors. Injuries were recorded for 3353, and 691 were held in tanks for delayed mortality studies. The size distribution of king crabs was bimodal (Fig. 1A); males exhibited modes near 62 and 135 mm CL, and females near 62 and 100 mm CL. Both sexes of Tanner crabs exhibited a single mode near 80 mm CW (Fig. 1B).

Overall survival

Overall survival was 21% (± 2.0%) for king crabs, and 22% (± 3.6%) for Tanner crabs (Table 2). Results for Tanner crabs are less accurate because fewer crabs were retained, especially from vitality group 1. Virtually no crabs were recorded as moribund after holding in live-tanks, regardless of initial condition; crabs either "recovered" or died. Potential sublethal effects, such as reduced feeding or growth rates due to injuries, could not be accounted for. At least one crab which

Table 2

Survival of crabs captured by Bering Sea trawls. Vitality codes: A = active, M = moribund, D = dead. Total number is weighted by subsampling factors. Letters in parentheses identify variables used in Equations 1 and 2.

	Vitality group		Retained subsample			
				Survivors		
Code	Weighted no. (N_v)	Proportion of total	No. kept	No.	Prop. (P_v)	Overall survival (no.)
King crab						
A	307	0.041	134	124	0.925	284
M	3617	0.486	455	158	0.347	1256
D	3521	0.473	28	0	0.000	0
Total	7445		617		0.207	1540
Standard error of estimate					0.010	
Confidence interval (± 2 SE)					0.020	
Confidence range					0.187–0.227	
Tanner crab						
A	154	0.009	1	1	1.000	154
M	5261	0.319	72	47	0.653	3434
D	11083	0.672	1	0	0.000	0
Total	16498		74		0.217	3588
Standard error of estimate					0.018	
Confidence interval (± 2 SE)					0.036	
Confidence range					0.182–0.253	

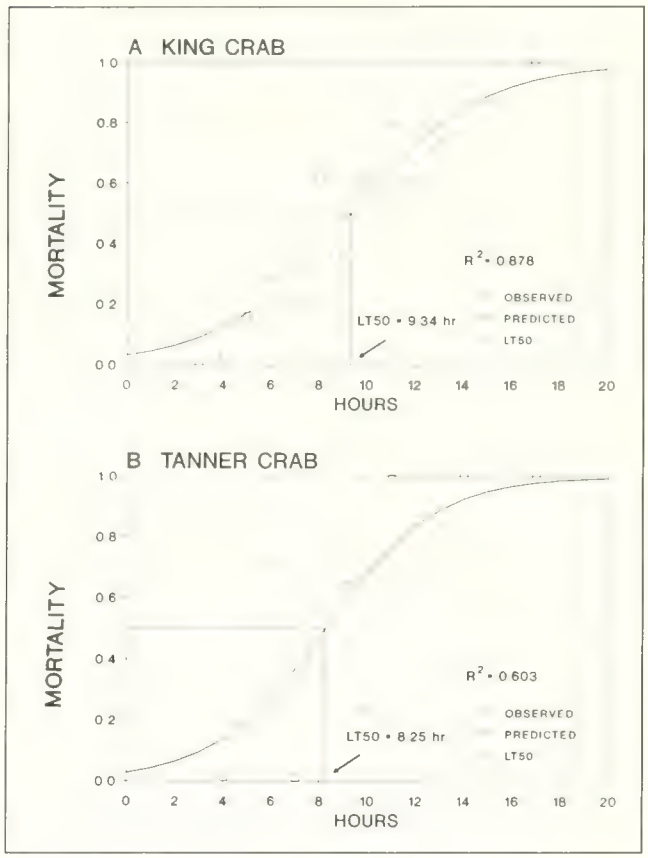

Figure 2

Logistic regression of immediate mortality vs. total time spent in captivity. Crabs were grouped into 1-hour intervals before analysis. (A) 6113 observations representing 7487 individuals. (B) 4645 observations representing 16498 individuals. Squares are observed data, solid lines represent predicted values.

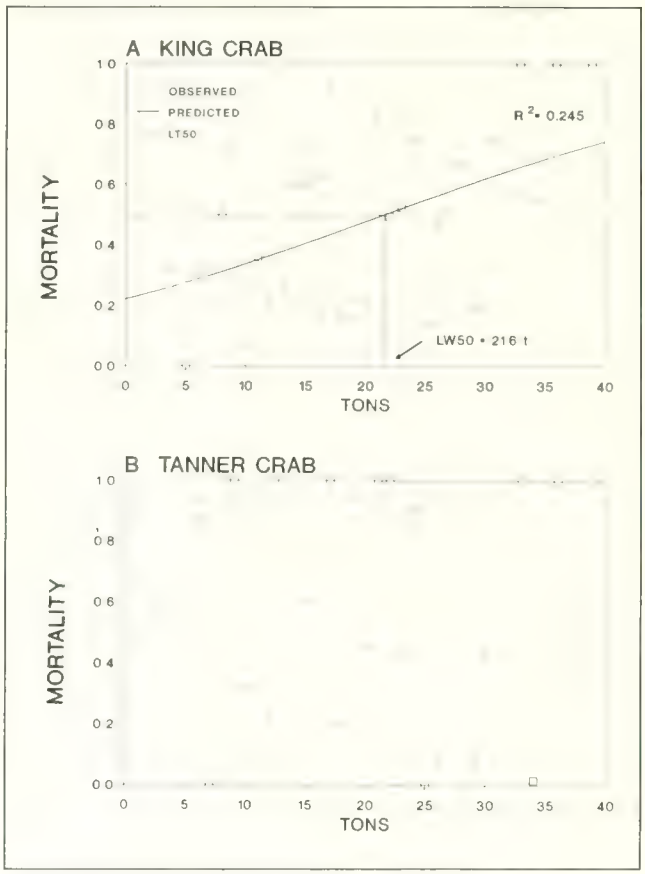

Figure 3

Logistic regression of immediate mortality vs. total weight of catch. Crabs were grouped into 1-t intervals before analysis. Squares are observed data, solid lines represent predicted values, which were incalculable for B.

had been tagged, held for observation, and released was recaptured with its tag still attached. Others may have been recaptured as well, but since most of the tags were removed prior to discarding the crabs, they could not have been identified as recaptures.

Effects of time in captivity and weight of catch

CAPTIME, the total time in captivity (prior to vitality/injury assessment) ranged from 3 to 17 hours (Fig. 2). The logistic fitting procedure indicated a significant relationship ($r^2 = 0.878$, $n = 13$, $\alpha < 0.001$) between CAPTIME and immediate mortality of king crabs (Fig. 2A); the relationship for Tanner crabs (Fig. 2B) was weaker but still significant ($r^2 = 0.603$, $n = 11$, $\alpha = 0.05$). The LT_{50}'s (time required for 50% immediate mortality) were 9.3 hours for king crabs and 8.3 hours for Tanner crabs.

Haul weights ranged from 4 to 39 t ($\bar{x} = 20.4$ t). The relationship between haul weight and immediate mortality for king crabs (Fig. 3A) was poor and non-significant ($r^2 = 0.245$). The relationship for Tanner crabs was so poor (Fig. 3B) that the iterative fitting procedure could not converge on a solution.

Shell conditions

Soft shell or molting crabs (shell condition 1) accounted for only about 1.1% of male king crabs, and <0.1% of females. All other females and most males were hardshell crabs (condition 2). About 9.4% of males were oldshell crabs (condition 3), and virtually all of these were above 100 mm CL. During the NMFS summer EBS survey in June of 1987 (Stevens et al 1987), 2.8% of males were soft or molting and many others were hardshell but recently molted. Immediate survival odds (ratio of survivors to deaths, Fig. 4) increased significantly ($X^2 = 81.63$, $p < 0.001$) with increased shell condition, i.e., hardness, but delayed survival was independent of shell condition ($X^2 = 0.60$, $p > 0.74$).

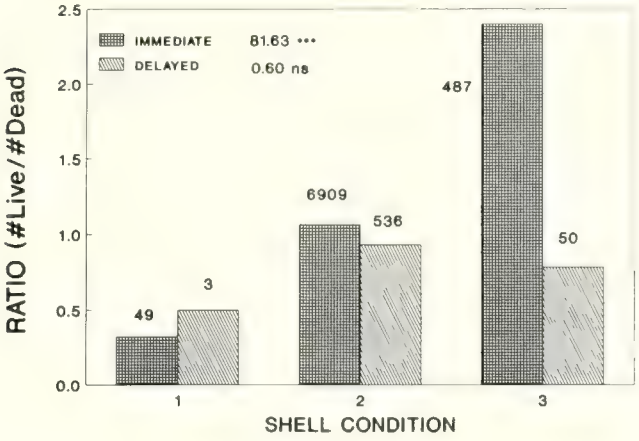

Figure 4

Effects of shell condition on immediate and delayed survival odds of king crabs. Condition coded as 1 = soft, 2 = new hardshell, 3 = old hardshell. Immediate effects are weighted by sample factors, delayed effects are not. *** indicates X^2 value significant at $p<0.001$. Sample size indicated above bars.

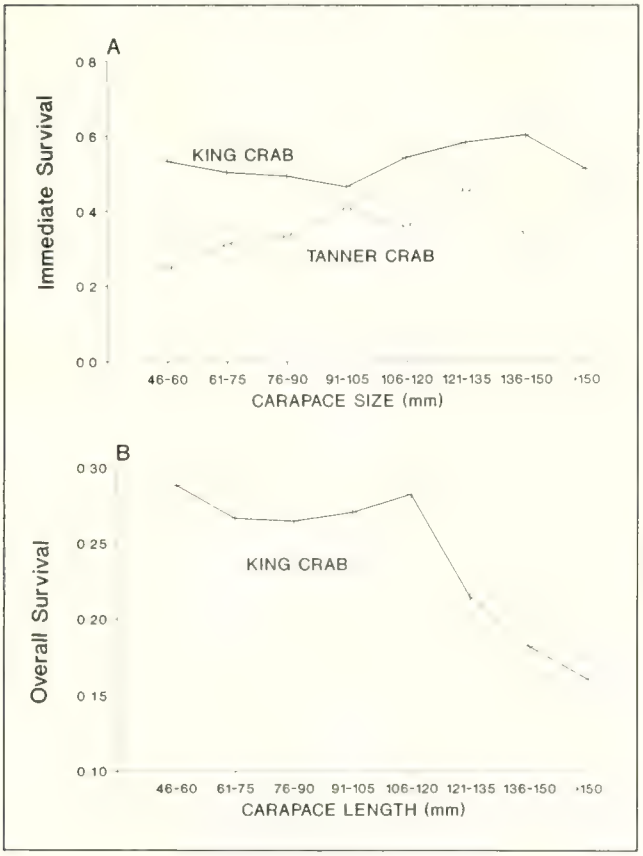

Figure 5

Effects of size on survival. (A) Immediate survival of king and Tanner crabs by 15-mm intervals of carapace length (king crabs) or carapace width (Tanner crabs). Numbers represented by each interval are 226–1520 king crabs and 71–9752 Tanner crabs. (B) Overall survival of king crabs, calculated as the product of immediate and delayed survival estimates.

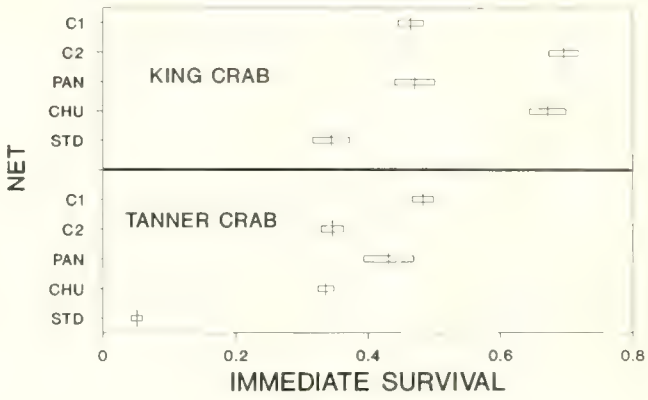

Figure 6

Effect of gear type on immediate survival of king and Tanner crabs. Vertical bar represents the mean; outer ends of box represent upper and lower confidence intervals, defined as $1.96(pq/n)^{1/2}$.

All female and most male Tanner crabs were hardshell (condition 2). Less than 0.3% of males were oldshell (condition 3), and less than 0.01% were softshell (condition 1). Low incidence of softshell and oldshell Tanner crabs prevented contingency table analysis due to too many empty cells.

Size effects

Immediate survival of king crabs did not vary much over the range of sizes captured (Fig. 5A). For Tanner crab, however, immediate survival increased slightly with size. Overall survival of king crabs (Fig. 5B) decreased markedly at sizes above 120 mm CL, mostly as a result of increased delayed mortality. Delayed mortality and overall survival could not be determined for Tanner crabs because of the limited number of observations.

Effects of gear type

Since survival was strongly related to CAPTIME, an analysis of variance was performed to determine if CAPTIME differed between the nets used. No significant differences were found ($F = 0.570$, $\alpha = 0.685$, df = 4181), so any differences in survival between nets can be attributed directly to the nets.

Immediate survival was least for the standard net (STD), for both species (Fig. 6). Nets C2 and CHU produced the best survival for king crabs, whereas C1 and PAN produced better survival for Tanner crabs. Overall, the experimental nets produced no clear differences in survival from the control nets for either species of crab. Extremely poor survival of Tanner crabs occurred in the standard net, and was probably the result of a biased vitality sample, which included

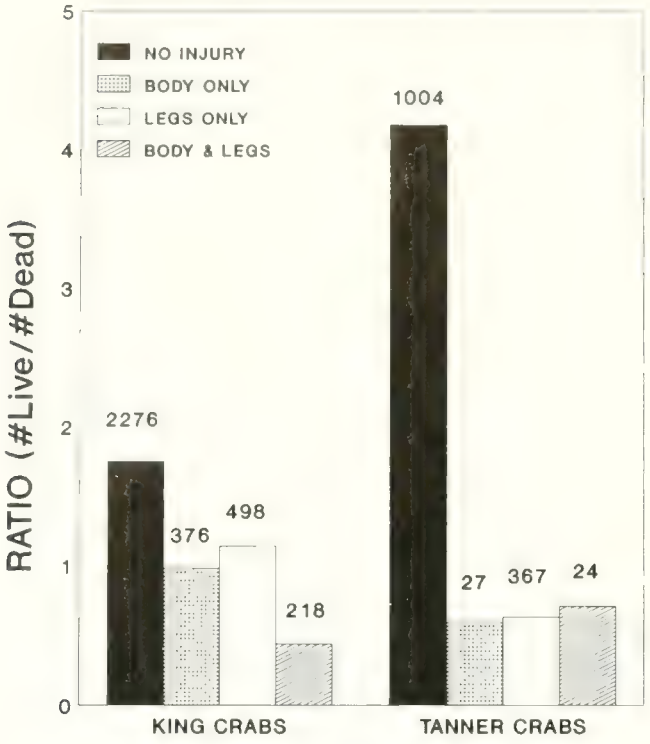

Figure 7

Effects of body and leg injuries on immediate survival odds (ratio of number surviving to number of deaths) of king and Tanner crabs. Sample size indicated above bars. Only injury-assessed crabs were used.

only six tows with this gear type, three of which had large sampling factors and mostly dead Tanner crabs. Delayed mortality was not compared between nets due to limited data.

Effects of injuries

A weighted number of 3368 king crabs and 1421 Tanner crabs were assessed for injuries. Figure 7 shows the survival odds (ratio of number alive to number dead) within each of four combinations of injury types: (1) none, (2) legs only, (3) body only, and (4) legs and body, calculated only for injury-assessed crabs. The majority of crabs suffered no detectable injuries, and had the best survival odds of 1.8 for king crabs and 4.2 for Tanner crabs. The most common type of injury for all crabs was leg injuries, which resulted in survival odds of 1.14 and 0.63 for king and Tanner crabs, respectively. Injuries to the body and combined body and leg injuries were less frequent, resulting in survival odds of 0.98 and 0.44, respectively, for king crabs, and 0.59 and 0.71 for Tanner crabs. Body injuries were more frequent but less serious among king crabs than Tanner crabs and were predominantly broken spines, which are more abundant and prominent on king crabs and thus more likely to be damaged. Body injuries of Tan-

Table 3

Contingency table analysis of interactions between delayed mortality, vitality, and injuries of king crabs. Null hypothesis was that row and column factors were independent. Data were taken only from survival experiment for king crab. Values are observed numbers of crab in each category; numbers in parentheses are calculated expected values or percent of grand total in row or column. All are 2×2 tables with 1 degree of freedom, and all are significant at $p<0.005$ (**).

	Vitality		Row		
Mortality	Active	Moribund	Sum	(%)	X^2 value
Vitality vs. delayed mortality					
Lived	124 (64)	158 (218)	282	(47.9)	138.6**
Died	10 (70)	297 (237)	307	(52.1)	df = 1
Column sum (%)	134 (22.8)	455 (77.2)		Total = 589	

	Injuries		Row		
	Uninjured	Injured	Sum	(%)	
Injuries vs. delayed mortality					
Lived	241 (221)	41 (61)	282	(47.9)	16.46**
Died	220 (240)	87 (67)	307	(52.1)	df = 1
Column sum (%)	461 (78.3)	128 (21.7)		Total = 589	
Vitality vs. injuries					
Active	118 (105)	16 (29)	134	(22.8)	9.77**
Inactive	343 (356)	112 (99)	455	(77.2)	df = 1
Column sum (%)	461 (78.3)	128 (21.7)		Total = 589	

ner crabs were typically broken or crushed carapaces which were associated with lower survival. In general, injuries were present in a greater proportion of dead crabs than live crabs. Combined body and leg injuries were most fatal for king crabs, whereas leg-only injuries accounted for the greatest number of dead Tanner crabs. The low survival odds for uninjured king crabs suggests that suffocation in the net or bunkers may have contributed strongly to their mortality.

Contingency table analysis (Table 3) showed that significant interactions occurred between vitality (VIT) and delayed mortality (DMORT; $X^2 = 138.6$), indicating that VIT was an excellent predictor of future survival or mortality for those king crabs held in survival tanks. Similarly, interaction between presence or absence of injuries (INJ) and DMORT ($X^2 = 16.46$) indicated that significantly more injured crabs died than were expected to, and that between VIT and INJ ($X^2 = 9.77$) suggests that injuries were partly responsible for observed vitality levels.

Loglinear analysis with DMORT as the dependent variable, and the interactions of DMORT with both VIT and INJ as independent variables (Table 4) indicated that the overall odds of survival were 2.087:1. These odds were increased by a factor of 4.713 for crabs coded as active (VIT = 1), and by a factor of 1.395 for crabs without injuries (INJ = 1). The total delayed survival odds for active, uninjured crabs equaled 13.73, the product of all three values. Similarly, survival odds for inactive, injured crabs were 0.317, the product of the mean odds (2.087), the odds for inactive crabs (0.212),

Table 4

Parameter estimates and survival odds for each factor in the logit model for king crabs. The dependent factor, DMORT, represents the mean survival odds (ratio of survivors to mortalities) and has no alternative outcome. Each interaction term has two alternative outcomes; alternative 1 represents cells with equal indices, i.e., values for Vitality and Injuries both equal 1 or both equal 2 (Table 5, lines 1 and 4), and alternative 2 represents cells with unequal indices (Table 5, lines 2 and 3). The survival odds for active crabs with no injuries (Vitality and Injuries = 1) is the product of antilogs for DMORT, DMORT × VIT_1, and DMORT × INJ_1, or 13.73. Survival odds are equal to the antilogs of 2(coefficient).

			Survival odds	
Factor	Coefficient	× 2	Alt. 1	Alt. 2
DMORT	0.368	0.736	2.087	
DMORT × VIT	0.775	1.550	4.713	0.212
DMORT × INJ	0.167	0.333	1.395	0.717
Sum		2.619	13.73	0.317

Table 5

Contingency tables used for calculating survival odds (ratio of survivors to mortalities) of king crabs and parameters of logit model. Expected odds are calculated as the product of individual parameters from Table 4. (A) Cells of table shown separately, with expected odds. Numbers in parentheses are factor codes. (B) Cells combined to show overall survival and survival odds calculated using alternative grouping procedures. Procedure 1 used only the criterion of vitality. Procedure 2 simulated the NMFS observer procedure by placing only active, uninjured crabs in category 1. Procedure 3 used only presence or absence of injuries as the criterion.

Cell category		Observed				Expected
Vitality	Injuries	Lived	Died	Proportion surviving	Odds	Odds
A Separate cells						
Active (1)	No (1)	110	8	0.932	13.750	13.727
(1)	Yes (2)	14	2	0.875	7.000	7.051
Morbid (2)	No (1)	131	212	0.382	0.618	0.618
(2)	Yes (2)	27	85	0.241	0.318	0.317
B Combined cells						
1 VIT only						
All active		124	10	0.925	12.4	
All inactive		158	297	0.347	0.532	
2 Observer procedure						
Active, uninjured		110	8	0.932	13.750	
Inactive or injured		172	299	0.365	0.575	
3 INJ only						
All uninjured		241	220	0.523	1.095	
All injured		41	87	0.320	0.471	

Table 6

Comparison of effects of body and leg injuries on immediate mortality of king crabs. (A) Loglinear analysis of immediate mortality (IMORT) as a function of body and leg injuries. Survival odds are equal to the antilog of 2(Coeff.), and are multiplicable. (B) Contingency table of data used for loglinear analysis. Numbers in parentheses are factor codes. Note that expected odds differ from observed odds, but not significantly. $\chi = 3.084$, with df = 1, and $p = 0.08$.

A Parameters of logit model

Factor	Coefficient	× 2	Antilogs Alt. 1	Alt. 2
IMORT	−0.017	−0.034	0.966	
IMORT by BODY	0.171	0.341	1.407	0.711
IMORT by LEGS	0.127	0.255	1.290	0.775
Sum		0.562	1.755	0.532

B Contingency table. U = Uninjured, I = Injured

Cell category		Observed				Expected
Body	Legs	Alive	Dead	Percent survival	Odds	Odds
U (1)	U (1)	1428	828	0.633	1.725	1.755
	I (2)	264	234	0.530	1.130	1.054
I (2)	U (1)	185	190	0.493	0.972	0.886
	I (2)	68	152	0.309	0.447	0.532

Table 7

Results of contingency table analyses of effects of types of leg injuries on immediate mortality (IMORT). Null hypothesis tested was independence of each injury type vs. IMORT. Expected ratio of percent live to dead crabs = 1.0 for all cases. Note that totals include uninjured as well as injured crab. ns = not significant at $p = 0.05$. *** significant at $p < 0.001$.

Type of injury	Number alive with injury	Percent of live crabs	Number dead with injury	Percent of dead crabs	Ratio % dead to % live	X
King crabs						
Autotomy	35	1.8	36	2.6	1.44	2.48 ns
Distal	284	14.4	313	22.3	1.55	34.86**
Proximal	29	1.5	113	8.1	5.47	88.06***
Total	1967		1401			
Tanner crabs						
Autotomy	47	4.8	123	27.4	5.67	149.85***
Distal	112	11.5	136	30.3	2.63	76.16***
Proximal	11	1.1	35	7.8	6.89	43.63***
Total	972		449			

and the odds for injured crabs (0.717). Alternatively, the log(ODDS) can be predicted as a linear function of each coefficient by substituting these values into Equation 5, e.g., for active, uninjured crabs,

$$\begin{aligned} \ln(f_{\dots}) &= 2(l_{\dots} + l_{\dots} + l_{\dots}) \\ &= 2(0.368 + 0.775 + 0.167) \\ &= 2.619 \\ \text{ODDS} &= \exp(2.619) = 13.74. \end{aligned}$$

Thus a 'good' vitality code of 1 was a better predictor of future survival odds than lack of injuries.

Table 5A shows the observed frequencies, percent survival, and survival odds, as well as the survival odds predicted by the logit model, for each combination of factors. Expected odds were calculated as the product of odds for each combination of interaction represented in Table 4. For instance, the expected survival odds for active (VIT = 1), injured (INJ = 2) crabs equalled 7.05, the product of odds for overall survival (2.087), active

crabs (4.713), and injured crabs (0.717). The likelihood ratio chi-squared value, calculated over all categories, was 2.30 with $p = 0.317$, indicating a good fit between the observed and expected survival odds.

In order to compare different methods of crab vitality assessment as tools for predicting future survival, cells of Table 5A were combined. Table 5B shows that using only vitality codes as an indicator of future survival resulted in survival estimates of 0.925 for VIT = 1, and 0.347 for VIT = 2, identical to those shown in Table 2. Simulation of the NMFS observer program procedure resulted in survival estimates which were slightly higher for both categories (0.932 and 0.365, respectively), but otherwise very similar. Use of only data on presence or absence of injuries did not provide adequate information about future survival.

Loglinear analysis was also conducted using immediate mortality (IMORT) as the dependent variable and the interactions of IMORT with body injuries (BODY) and leg injuries (LEGS) as the independent variables (Table 6A). The parameter for mean survival odds was 0.966, or about 1:1. Absence of body injuries increased the odds of survival by a factor of 1.407; their presence decreased survival odds by 0.711. Absence of leg injuries increased survival odds by a factor of 1.290. Coefficients for IMORT × BODY and IMORT × LEGS were not significantly different. Expected odds differed slightly but not significantly ($\chi^2 = 3.084$, df = 1, $p = 0.08$) from observed odds (Table 6B).

Evidence of recent leg autotomy was not significantly associated with immediate mortality of king crabs ($X^2 = 2.48$; Table 7A). However, leg injuries which occurred distal to the autotomy plane were significantly ($X^2 = 34.86$) associated with IMORT, as were those which occurred proximal to it ($X^2 = 88.06$). Proximal injuries had the greatest effect, increasing deaths above the expected proportion by a factor of 5.47. All three types of injuries were significantly associated with IMORT for Tanner crabs (Table 7B). Immediate survival odds, expressed as the ratio of live/dead crabs, decreased significantly with the number of legs injured for both king ($X^2 = 86.5$) and Tanner crabs ($X^2 = 225.3$; Fig. 8A). Delayed survival odds also decreased significantly with the number of injured legs for king crabs ($X^2 = 17.0$), but not Tanner crabs ($X^2 = 4.8$), perhaps due to inadequate sample size for the latter.

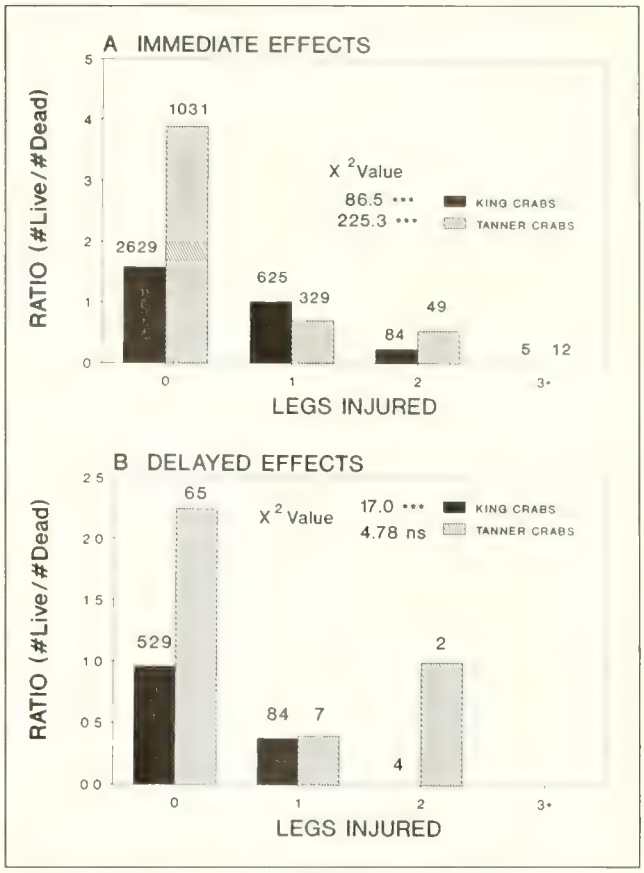

Figure 8

Effects of multiple leg injuries on survival odds of king and Tanner crabs. *** indicates X^2 value significant at $p<0.001$. Sample size indicated above bars.

Discussion

The results of this study show that, although the majority of crabs died as a result of capture incidental to commercial trawling operations, a significant proportion (>20%) can survive the process. The major factors associated with increased crab mortality were shell condition and time in captivity (CAPTIME) prior to recovery. The present study was conducted in August, when both king and Tanner crabs are typically hard-shelled. However, molting for both species usually occurs from January through June, coincident with the season in which most sole trawling occurs in the EBS, so mortality due to molting would probably be greater during the normal fishery. Processing times observed in this study ranged from 0.8 to 12.5 hours, which may have been longer than normal due to the sampling operation, so they probably caused higher than normal mortality. If average processing times for the commercial fishery are less than those observed here, expected mortality would also be less. The study conditions also differed from normal operations in that crabs were retained for several hours after recovery for examination, whereas those recovered during normal operations would have been placed on discard conveyors and returned to sea sooner, probably increasing their survival rates.

For king crabs, the relationship between time in captivity and immediate mortality was strong enough that knowledge of average processing times for a particular trawl fishery could be used to estimate overall survival of crabs. It can also allow estimation of the effects of reduced captivity time on survival. In this study, immediate survival (0.527) and delayed survival (0.472) of king crabs were approximately equal (Table 2). For illustrative purposes we can assume that this equivalency is a general phenomenon, and these two aspects of survival vary proportionally, since increased stress should result in increases in both immediate and delayed mortality. Based on this assumption, the estimated overall survival at the median lethal time of 9.3 hours would be approximately 0.5×0.5 or 0.25, which is very close to the value of 0.21 estimated in Table 2, but differs slightly because the latter was calculated in a stratified manner over all conditions rather than just representing the median lethal time. Overall survival could theoretically be doubled to 50% by reducing CAPTIME such that immediate (and consequently delayed) survival was equal to $0.5^{1/2}$, or 0.71, i.e., by reducing mortality to 1–0.71, or 0.29. Solving the logistic equation (Eq. 3) for X results in:

$$X = X_{50} \quad \{\ln[(1 - M)/M]\}/r \qquad (3.1)$$

Substituting $0.29 = M$ (as determined above), $9.34 = X_{50}$, and $0.367 = r$ (the latter two values are fitted parameters from the logistic model for king crab survival) results in $X = 6.90$ hours. Thus, for this example, reducing the median total time in captivity from 9.34 to 6.9 hours (a 26% reduction) would increase the immediate and delayed survival rates from 0.50 to 0.71 (a 42% increase), and consequently increase the overall survival to a value equal to the square of immediate survival, $0.71 \times 0.71 = 0.50$, i.e., a 100% increase in overall survival, assuming immediate and delayed survival to be approximately equal, as stated above.

Reduction of CAPTIME, the time crabs spend in the trawlnet or the processing bins, could be accomplished by reducing either towing time, processing time, or both. If towing time cannot effectively be reduced (and may in fact need to be increased to efficiently use the experimental trawls because of reduced fish catch rates) then delay time (between net haulback and delivery to the processing vessel) and processing time (time spent on deck or in the bunkers prior to recovery) should be reduced as much as possible. This could be achieved through better communication and coordination between catcher and processor vessels in order to more evenly distribute deliveries to the processor over time, and reduce or prevent a backup in processing. Towing time may actually contribute less to mortality than processing time, since fish and crabs are less densely packed in the net during towing, and have access to free flowing water. However, neither of these variables (towing or processing time) provided a significant predictive relationship by themselves. Once the codend is recovered on deck, the packing density and pressure within the codend increase greatly and probably contribute substantially to mortality of fish and crabs therein.

Observers placed aboard trawlers by NMFS or the State of Alaska have a variety of tasks to perform, and assessing crab vitality has usually been one of low priority. If one objective were to determine the proportion of crabs that clearly have the best chance of survival, then a two-step process using both vitality and the presence of injuries, such as that currently used by the NMFS observer program, is a better method, as crabs which fell into the "best" category of this scheme exhibited 93.2% survival. Even better predictions could probably be made if degrees of injury (e.g., none, mild, severe) were coded and used to predict survival. However, if the object were to predict survival using the quickest and most efficient method of assessment, then use of vitality alone might be the best choice, as it indicated similar survival (92.5%) for the top category and could be assessed adequately in seconds, whereas a comprehensive assessment for injuries required a deliberate, systematic examination, consuming more time than may be available, given the priority of the task. Even then, some injuries, such as minor cracks in the carapace, were easy to miss.

Despite the quantity of data collected on injury types and severity, there was no clear, unambiguous relationship between injuries and mortality. The overall physical condition of crabs, which could be assessed by activity level, was a better indicator of future survival than injuries. Leg injuries were only slightly more fatal than bodily injuries to king crabs. Both immediate and delayed mortality increased with the number of legs injured, and proximal injuries to legs were more fatal than distal injuries, which was not unexpected since bleeding from the coxa or basi-ischium (leg segments which are proximal to the autotomy plane) would likely be more difficult for the crab to stop than bleeding from a more distal segment, which could be autotomized at a later time. In our experience, though, it was uncommon for crabs that had injured legs at the time they were examined to autotomize them in the live tanks. If autotomy had not occurred soon after the injury, and prior to examination, it was less likely to do so after a day or two. However, this is a subjective observation and was not documented, because injuries were not reassessed prior to release. The poor relationship between injuries and death suggests that other factors, such as exposure or suffocation, may have played a significant role in determining survival of crabs.

In an attempt to simulate the effects of culling crabs in the directed, winter-season pot fisheries, Carls and O'Clair (1990) documented the effects of exposure of ovigerous female king and Tanner crabs to various combinations of time and air temperature (max. 40 min. at −19°C). They found that both mortality and righting time were inversely proportional to exposure, expressed in terms of degree-hours, but neither response occurred in air temperatures above 0°C. Their conditions contrasted with this experiment; although water and air temperatures were not recorded, 30-year mean August seawater temperatures in the area where this experiment was conducted have been 2–5°C on bottom and 8–9°C at surface (Ingraham 1983), and air temperatures were probably above 10°C, so no negative degree exposures occurred. However, during the winter trawl fishery such exposures might occur, although most crabs would be insulated by the surrounding catch in the net or processing bins.

Carls and O'Clair (1990) also found that exposure-related mortality of king crabs was delayed, occurring 16–128 days after exposure, and was usually associated with ecdysis; in contrast, 50% of their Tanner crab mortality occurred within the first 24 hours. Although crabs were not retained over 48 hours in the present experiment, and no ecdysis occurred, exposures were not as severe either.

Location of leg breaks was found to be related to mortality of stone crabs *Menippe mercenaria* by Simonson and Hochberg (1986). They studied the effects of exposure and claw breakage on survival of stone crabs and found that breakage on either side of the breakage plane resulted in significantly higher mortality than breaks on the plane. Mortality also increased with severity of the break, and length of exposure, from 2 to 6 hours. Severity of breaks also increased with exposure time prior to breakage. In their study, claw breakage was intentional rather than accidental, as fishermen remove the claws for sale and return the live, clawless crab to the sea.

Crabs subjected to trawl capture and subsequent release probably also suffer some sublethal effects, but they could not be documented in this study. Brown and Caputi (1985) studied the effects of exposure and leg loss on growth of sublegal rock lobsters *Panulirus cygnus*, and found that exposure for periods of 15, 30, and 60 minutes resulted in decreased growth at the next molt of 0.8–2.3 mm, or 1.2–3.3% of carapace length. In addition, the growth increment was reduced by 0.48 mm, or about 0.7%, for each appendage missing. Carls and O'Clair (1990) also found that female king crabs exposed to subzero air temperatures showed decreased growth at subsequent molts. Other sublethal effects included reduced feeding rates and increased limb autotomy by female Tanner crabs.

The recapture of a tagged and released crab indicates that such multiple captures of discarded crabs may be common in this type of intensive fishery. Recaptured crabs would probably have lower survival rates than crabs captured and released only once, due to the cumulative effects of stress and injuries. However, there is no evidence suggesting that the rate of recapture during the experiment differed from the normal conditions of the commercial fishery, so the calculated survival rates may adequately incorporate any effects of recapture.

Smith and Howell (1987) studied the effects of trawl capture on American lobsters *Homarus americanus* in Long Island Sound and found that the incidence of damage varied seasonally from 0 to 14%, and was greater during months when molting was occurring. Immediate plus delayed mortality ranged from 1% to 21%, depending upon season also. In contrast to this report, they found that uninjured lobsters, and those with autotomized claws rarely experienced delayed mortality, and that seasonally warm seawater temperatures were associated with increased delayed mortality independent of damage. The conditions to which lobsters were exposed differed greatly from those encountered by king crabs, however, as the lobsters were commonly sorted out of the catch in less than an hour, as opposed to times of 3–17 hours for crabs in this study.

The effect of discarding crab via conveyor belts and discard chutes from the factory was not examined, and could inflict further injury upon crabs via entanglement in machinery or damage upon impact with the water surface, 3–6 m below the discard chute.

The estimated catch of 88000 red king crabs and 751000 Tanner crabs *C. bairdi* by the Bering Sea JV fishery in 1988 (Berger and Weikart 1989) amounted to 0.22% and 0.11% of the total estimated abundance of those two species, respectively, in the Bering Sea that year (Stevens et al. 1988). Even though the amount of bycatch in the domestic fishery is unknown, it is unlikely that the total bycatch exceeded 0.5% of the population for either species, largely as a result of restrictions on bycatch. Removals of this magnitude are well below the ability of the NMFS crab survey to detect, and probably have no significant biological impact. The possibility of additional, unseen mortality of crabs due to trawling has largely been discounted by submersible studies (West 1987, Highliners Association 1988) in which the observed trawls made little or no contact with the sea bottom, caused no observable injuries to crabs contacted, and no injured or dead animals were observed in the wake of the net.

Nevertheless, the issue of bycatch mortality is of great concern to the fishing industry, and the North Pacific Fishery Management Council has developed a

policy of reducing bycatch mortality as much as possible. To that end, the most useful results of this study were, first, that crab mortality increased with CAPTIME, so reduction of CAPTIME should be a high priority. Second, reduction of king (and probably Tanner) crab mortality could be achieved by conducting the trawl fishery during periods of the year when molting activity is at a minimum.

Summary

1 Over 50000 crabs were measured during the study. Vitality was recorded for over 10000, injuries for 3353, and delayed mortality for 691.
2 Overall survival was estimated to be 21% (±2.0%) for king crabs and 22% (±3.6%) for Tanner crabs.
3 Overall survival of king crabs declined at sizes above 120 mm CL. Overall survival could not be determined for Tanner crabs, but immediate survival showed a slight increase with size.
4 Immediate mortality of king and tanner crabs increased in direct proportion to time in captivity, but was poorly related to weight of the catch.
5 Immediate survival odds for king crabs increased significantly with shell age.
6 No clear difference in survival was apparent between the net types for either king or Tanner crabs.
7 Delayed mortality was shown to be dependent on both vitality and injuries, with vitality being the best predictor. Observation of injuries did not contribute substantial additional information concerning future (48-hour) survival.
8 Leg and body injuries contributed about the same amount to immediate mortality, but mortality increased with number of legs injured, and injuries to leg segments proximal to the autotomy plane were more serious for king crabs but not for Tanner crabs.

Acknowledgments

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Abstract.– Age-0 weakfish *Cynoscion regalis*, were sampled from the Chesapeake Bay–York River estuary in 1983 and 1984 to test for the existence of multiple cohorts and compare growth rates. In both years juveniles were first collected in the estuary in late July, were significantly more abundant from August to mid-October, but were uncommon by the end of October. Significantly more weakfish were collected in 1983 than in 1984. Daily ages were determined based on scale circuli. Cohorts were separated by local minima in birthdate distributions: cohort 1 hatched before 16 July 1983, cohort 2 (16 July–15 August 1983), cohort 3 (15 August–9 September 1983), cohort 4 (5 May–20 June 1984), and cohort 5 (5 July–1 September 1984). Compared with other cohorts, groups 1 and 4 had significantly slower growth rates (0.83 and 0.84 mm/day, respectively), while cohort 5 had a significantly faster growth rate (1.09 mm/day), and cohorts 2 and 3 were intermediate (both at 0.96 mm/day). Weakfish juveniles were transient and migrated up the estuary as they grew, as indicated by cohort and age distributions over stations and dates. Also, cohorts appeared to partition the estuary; for example, cohort 1 was more common up the estuary compared with other cohorts. The existence of multiple cohorts with significantly different growth rates and apparent differential habitat use suggests that the juvenile stage of weakfish may show high variability in survival, and the presence of multiple cohorts within a single year-class must be considered in the estimation of juvenile recruitment to the adult population.

Differential Growth Among Cohorts of Age-0 Weakfish *Cynoscion regalis* in Chesapeake Bay*

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A common assumption of early-life-history studies of fishes has been that the most critical period for survival occurs during egg and larval stages, thereafter juvenile fish show fairly constant growth and mortality rates (Cushing 1975, Williams 1983, Hewitt et al. 1985, Victor 1986). However, postmetamorphic survival may be highly variable and we may need to extend the critical survival concept to include the juvenile stage of fishes to better understand year-class variability (Walline 1985, Eckert 1987, West and Larkin 1987). The existence of multiple cohorts within age-0 fishes may help explain variable annual survival of juvenile fishes (Buchanan-Wollaston and Hodgson 1929, Cooper 1937, Lambert and Ware 1984). Survival is difficult to estimate without information on residency time, but growth rate can be used as an indicator of potential survival because it is an integrator of most other environmental factors. For example, those individuals that grow the fastest will increase their chances of survival because they grow through the size range vulnerable to predators at a faster rate (Tonn and Paszkowski 1986, Post and Prankevicius 1987, Post and Evans 1989). Faster growth also implies that they are more physically fit, e.g., larger individuals may be able to survive overwinter stress better than smaller individuals (Conover and Ross 1982, Takita et al. 1989).

The key to evaluating variation in growth rates among age-0 fishes is the ability to age young fish. Larval and juvenile fishes have been assigned daily ages by length-frequency analysis, a somewhat imprecise method (MacDonald 1987), or by counting microincrements in otoliths (see reviews: Campana and Neilson 1985, Jones 1986). Daily aging of juvenile weakfish *Cynoscion regalis*, by otolith microincrements was unreliable (Szedlmayer 1988), but a new method of counting circuli in scales appears promising (Szedlmayer et al. In press). The present study uses this new method to test for multiple cohorts within age-0 weakfish, and to estimate growth rates and differential habitat use by fish collected in the Chesapeake Bay–York River estuary, Virginia.

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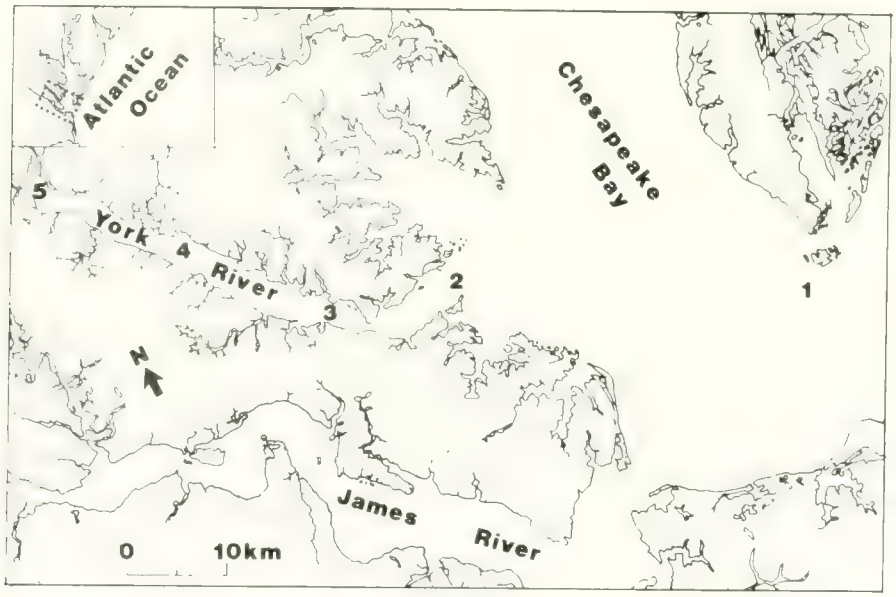

Figure 1
Station locations for age-0 weakfish collections in Chesapeake Bay–York River, VA. Station 1 (0 km, bay entrance), station 2 (30 km up estuary), station 3 (45 km up estuary), station 4 (63 km up estuary), and station 5 (75 km up estuary).

Materials and methods

Juvenile weakfish were collected at night (Leber and Greening 1986) with an otter trawl (4.9 m, 19-mm mesh wings, 1.5-mm codend). In 1983, collections were made weekly at four stations in the York River estuary, Virginia, from 12 July to 26 October: stations 2, 3, 4, and 5; 30, 45, 63, and 75 km up the estuary from the Bay entrance, respectively (Fig. 1). Station 1 was added at the mouth of Chesapeake Bay in 1984, while collections at Station 4 were discontinued (Fig. 1). In 1984, collections were made every 2 weeks from 21 June to 16 November. Repetitive, 2-minute trawls were made at each station until 30 fish were captured or until 6 tows were completed. Salinity and temperature were recorded with a Beckman conductivity meter at the bottom at each station.

Weakfish were stored in 70% ethanol. Standard lengths of preserved fish were recorded with calipers to the nearest 0.1 mm. At least three scales were taken from just below the midbody lateral line curve (usually five) and circuli were counted according to Szedlmayer et al. (In press). When three scales could not be taken, the fish was not used. The highest scale circuli counts from individual weakfish were used for age estimations. Age was estimated, based on daily scale circuli counts, plus a 26-day estimate of the time delay from hatching to first circulus formation. Also, if fish were <14 mm SL (prior to scale formation), age was estimated by quadratic regression of size on age based on laboratory-reared fish (for validation of daily circuli deposition and further details of this method, see Szedlmayer et al. In press). Subsequently, birthdates were backcalculated by subtraction of estimated age from date of capture. Birthdate frequency distributions were smoothed with a 3-day moving average. Cohorts within a year-class were identified by local minima in the birthdate frequency distributions (Graham and Townsend 1985). After separation of fish into their respective cohorts, growth rates were estimated by linear regression of standard length on age. Migration patterns within the estuary and differential habitat use by cohorts were suggested by abundance modes over stations and collection dates, mean ages by stations, and cohort-specific age-frequency distributions over stations and collection dates.

A 0.05 level of significance was used for analysis of variance and covariance. Nonparametric analysis of variance by ranks of main effects (year, station, date) was used to test for abundance differences (catch-per-unit-effort = number/2-minute trawl tow). Analysis of covariance was used to test for significant differences in growth rates among cohorts. Analysis of variance was used to test for age differences among stations, pooled over dates. After significance was determined, Student-Newman-Keuls test was used to show specific differences at a 0.05 level of significance or a 0.10 level if a type II error resulted at the former level (Zar 1984).

Results

Salinity variation was associated with station, while temperature variation was associated with season. As

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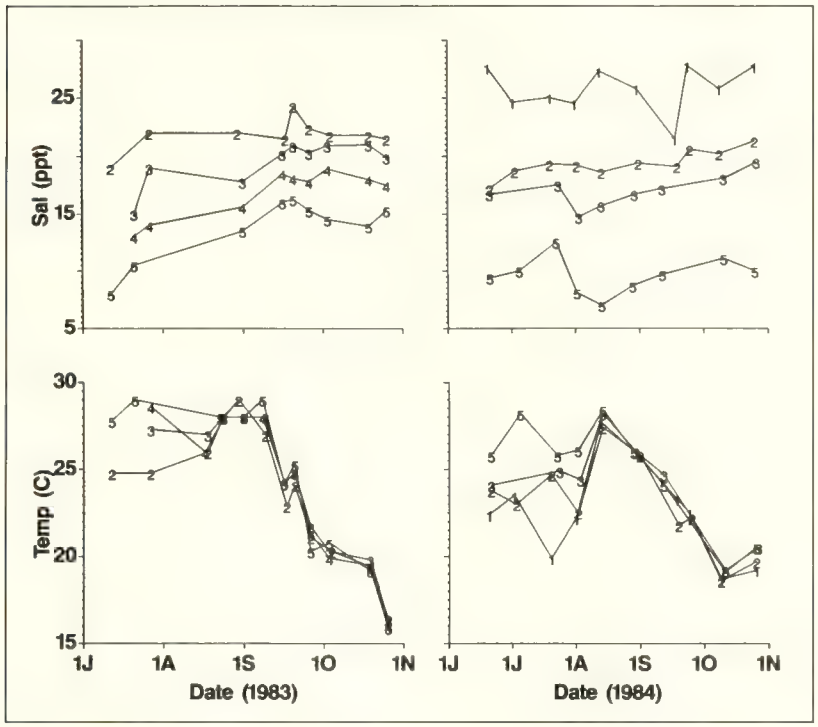

Figure 2
Salinity and temperature in Chesapeake Bay–York River, VA, from all collections, 1983 and 1984. Numbers on each line refer to station and mark data points.

expected, salinity was highest at station 1, and decreased up the estuary. Salinity was slightly higher at stations 2 through 5 in 1983 compared with 1984 (Fig. 2). Little difference was detected in temperature among stations, except in June and July 1984, where temperatures were 4–5°C warmer at the upper estuary stations. Seasonally, temperature ranged 16–29°C in 1983, and 18–29°C in 1984 (Fig. 2).

Weakfish catch-per-unit-effort was significantly greater in 1983 than in 1984 (Table 1; Fig. 3). Seasonally, fish were uncommon in July samples, significantly more abundant in samples taken from mid-August to mid-October, but by the end of October were few in number. No significant differences in catch-per-unit-effort were detected among stations. Lack of replication in some cells (i.e., one 2-minute tow resulted in >30 weakfish) prevented testing for interaction effects between station and date. However, although not statistically significant, there was an apparent pattern: in both years fish were first abundant down estuary, and as the season progressed became more abundant further up the estuary (Fig. 3).

In 1983, 845 fish were aged out of 993 collected, and in 1984, 361 fish were aged out of 571 collected, by the scale circuli method. An additional 98 fish were <14 mm SL (prior to scale formation), and ages were estimated by applying a quadratic regression of known age on standard length from laboratory-reared weakfish (Szedlmayer et al. In press).

Table 1
Juvenile weakfish CPUE (no./2-minute tow) from the Chesapeake Bay and York River, VA, based on three-factor (main effects only) nonparametric ANOVA by rank abundance. Student Newman Keuls test (SNK) was used to show specific differences, denoted by different letters (0.05 level).

Source of variation	df	MS	*F*	*P*>*F*
Year	1	5138.7	16.90	0.0001
Station	4	389.4	1.28	0.2870
Date	7	1216.4	4.00	0.0012
Error	61	303.7		

	CPUE	Trawls	SNK-test
Date			
16–29 July	1.2	20	C
30 July–12 Aug.	0.8	16	C
13–26 Aug.	5.0	60	A B
27 Aug.–9 Sept.	7.1	51	A
10–23 Sept.	8.5	37.5	A
24 Sept–7 Oct.	5.1	52	A
8–21 Oct.	4.4	46	A B
22 Oct.–4 Nov.	1.6	49	B C
Year			
1983	6.5	152.5	A
1984	3.2	179	B

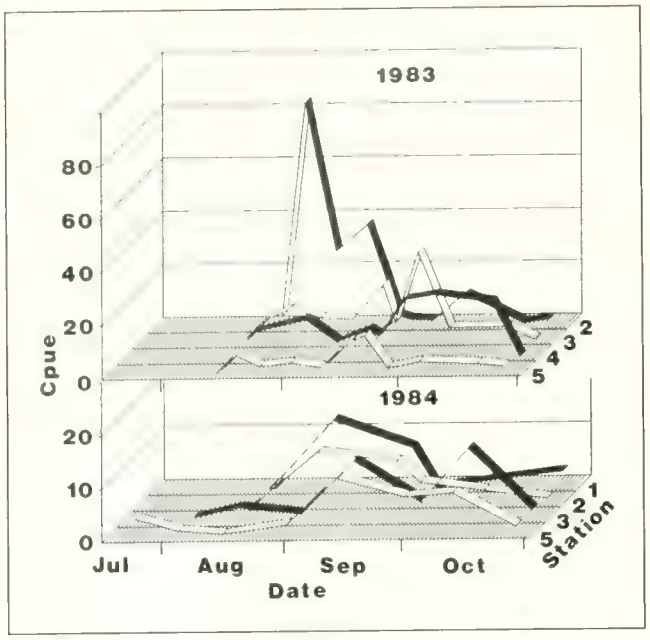

Figure 3

Standardized abundance of age-0 weakfish (CPUE = number/2-minute tow) by station and date in Chesapeake Bay–York River, VA.

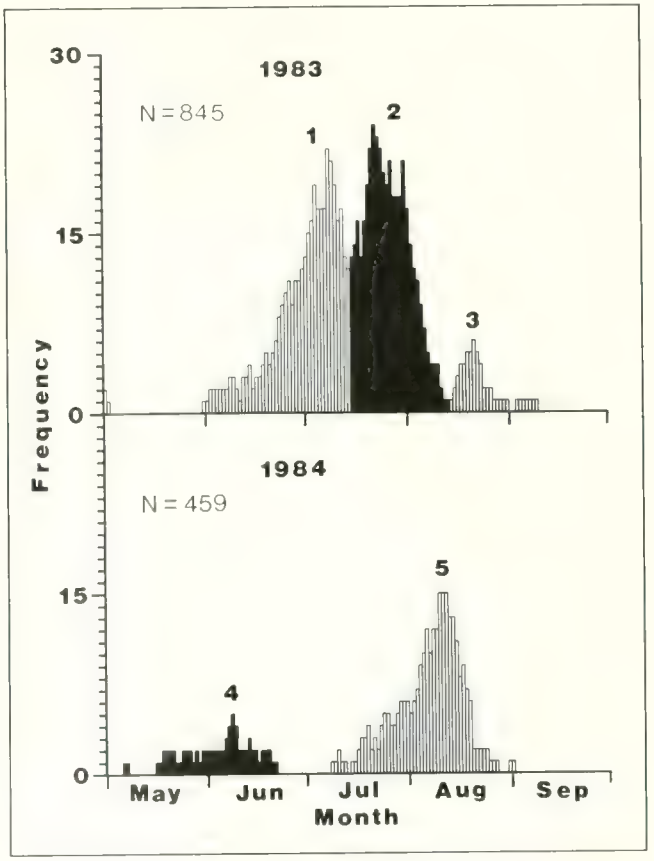

Figure 4

Birthdate frequency distribution of age-0 weakfish cohorts in Chesapeake Bay–York River, VA, based on a 3-day moving average. Numbers at the peaks of the distributions refer to cohorts (separated by open and shaded bars).

Multiple cohorts were apparent in both years. The birthdate frequency distributions showed three cohorts in 1983, and two cohorts in 1984 (Fig. 4). Cohorts were defined in 1983 as follows: cohort 1 hatched before 16 July, cohort 2 between 16 July and 15 August, and cohort 3 after 15 August. Another cohort may have been present in 1983 before 18 June, but these fish were relatively few in number and subsequently pooled with cohort 1. In 1984 two cohorts 4 and 5 were defined as those that hatched before 30 June and those after, respectively (Fig. 4).

Weakfish growth rates were significantly different among cohorts within years, and between years (Table 2). Cohorts 1 and 4, both early-season cohorts, had the lowest growth rates and were not significantly different from each other. Cohorts 2 and 3 had intermediate growth rates, and cohort 5 had the fastest growth rate compared with all other cohorts (Table 2).

After separation of individual weakfish into their respective cohorts, a similar pattern of movement by each cohort was apparent: up the estuary with age and season (Figs. 5, 6). For example, the youngest fish in cohort 2 were first most abundant in the lower estuary (stations 2 and 3), and as the season progressed older fish from this cohort were more abundant up the estuary at the same location where few individuals of this cohort were collected earlier (station 4 in August vs station 4 in September 1983; Fig. 5). Cohort 4 showed the only difference from the above migration pattern.

Table 2

Growth rates (mm/day) of individual age-0 weakfish cohorts. Analysis of covariance of standard length on age with cohort as the covariate (0.05 level). Student Newman Keuls test (SNK-test) was used to show specific differences, denoted by different letters (0.10 level).

Source of variation	df	MS	F	$P>F$
Cohort	4	20178.39	1597.8	0.0
Age	1	448840.88	35540.4	0.0
Age × Cohort	1	1686.94	133.6	0.0
Error	1294	12.63		

Cohort	Growth rate	R^2	N	SNK-test
1	0.83	0.95	383	A
2	0.96	0.96	405	B
3	0.96	0.94	57	B
4	0.84	0.96	75	A
5	1.09	0.98	384	C

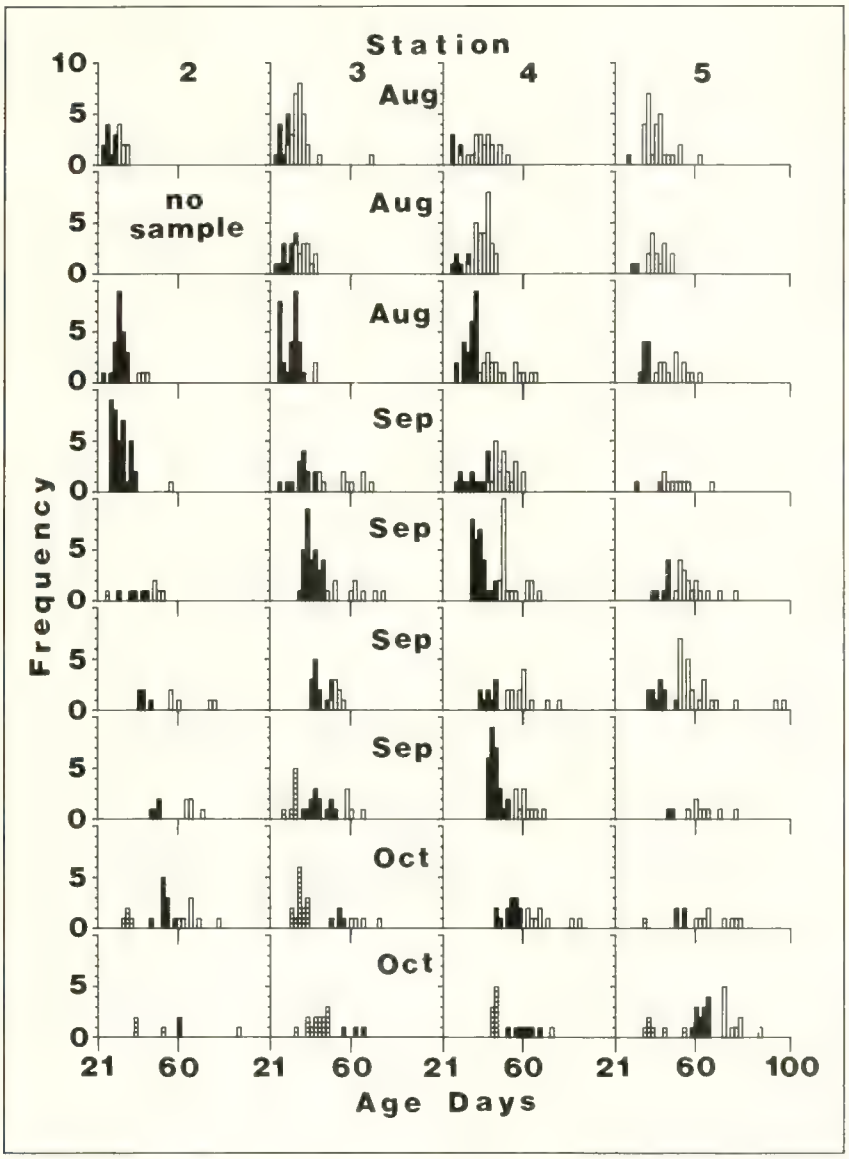

Figure 5
Age of weakfish estimated from scale circuli for 1983, versus frequency (number/2-minute tow), by station, date, and cohort in Chesapeake Bay–York River, VA. Cohort 1 = open bars, cohort 2 = solid bars, and cohort 3 = cross-hatched bars.

The earliest recruits in cohort 4 were first collected at the upper estuary station (5), then appeared to spread down the estuary in subsequent collections (Fig. 6). An up-the-estuary movement with age pattern was also supported by the mean ages associated with each station, because weakfish were significantly older as the distance from the Bay mouth station (1) increased (Table 3), and by an increase in total catch-per-unit-effort up the estuary with season (Fig. 3). Different cohorts appeared to segregate habitats. In 1983, cohort 1 was more common further up the estuary compared with other cohorts, while cohort 2 dominated the middle habitats (Fig. 5). Cohorts 3 and 4 were lower in abundance and it is difficult to suggest a pattern, while cohort 5 appeared dominant at all stations after August 1984 (Fig. 6).

Discussion

To our knowledge this is the first clear identification of multiple age-0 weakfish cohorts, and they showed significantly different growth rates and appeared to partition habitats. Earlier, Massmann (1963) suggested the existence of age-0 multiple cohorts from bimodal length-frequency distributions, but did not examine growth rates or differential habitat use. Except for two early studies (Buchanan-Wollaston and Hodgson 1929, Cooper 1937) reports of multiple cohorts in the juvenile stage of fishes are few (Shlossman and Chittenden 1981, DeVries and Chittenden 1982, Crecco and Savoy 1985, Kumagai et al. 1985, Eckert 1987, Isely et al. 1987, Wicker and Johnson 1987). This may be because of the difficulty of aging juvenile fishes (Geffen 1986,

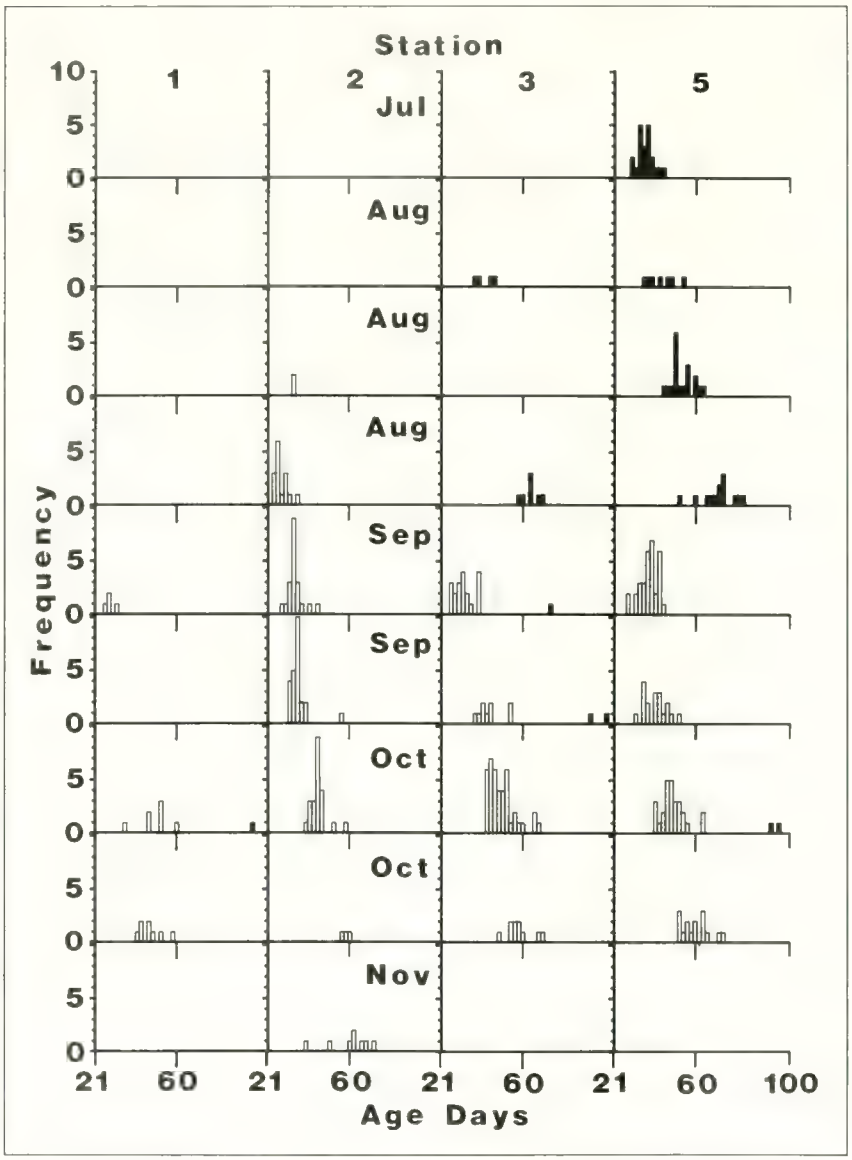

Figure 6

Age of weakfish estimated from scale circuli for 1984, versus frequency (number/2-minute tow), by station, date, and cohort in Chesapeake Bay–York River, VA. Cohort 4 = solid bars, cohort 5 = open bars.

Table 3

Comparison of weakfish age by station, pooled over dates, based on ANOVA (0.05 level). Student Newman Keuls test (SNK-test) was used to show specific differences, denoted by different letters (0.05 level).

Source of variation	df	MS	F	$P>F$
Station	4	37126.0	123.6	0.0001
Error	1299	300.3		

Station	Age	N	SNK-test
1	26.1	104	A
2	50.2	248	B
3	57.1	56	C
4	61.8	279	D
5	66.8	327	E

Essig and Cole 1986, Jenkins 1987, Post and Prankevicius 1987), or that fewer studies have examined postmetamorphic life stages because juvenile survival after metamorphosis was considered relatively constant compared with larval stages (Cushing 1975, Victor 1986). Constant growth and mortality in postmetamorphic juveniles have been questioned; for example, Wicker and Johnson (1987) showed a large increase in the rate of mortality in age-0 largemouth bass *Micropterus salmoides* when juveniles shift from an invertebrate to fish diet. Van der Veer and Bergman (1987) suggested that mortality due to predation by shrimp *Crangon crangon* on newly settled juvenile plaice *Pleuronectes platessa* may be significant and thus account for the difficulty of predicting year-class abundance based on egg and larval surveys. However,

studies of American shad *Alosa sapidissima* suggested that year-class strength is established before the juvenile stage (Crecco et al. 1983, Crecco and Savoy 1984, Crecco and Savoy 1985). Consequently, the importance of critical periods during the juvenile stage may be species-specific. Because several age-0 cohorts of weakfish showed variable growth rates and distribution, survival of the juvenile stage of this species should not be assumed to have a constant rate.

Different population parameters among cohorts are difficult to relate to salinity and/or temperature differences observed among stations. First, juvenile weakfish are transient, as observed over the present study area and in earlier studies (Harmic 1958, Massman 1963, Chao and Musick 1977, Shepherd and Grimes 1983), and until accurate residency times can be estimated it may be ineffective to ascribe cohort differences to particular habitat parameters. Second, other factors not measured in the present study, e.g., prey abundance, turbidity, currents, and predation may also be linked to cohort differences.

In comparison with other juvenile fish, age-0 weakfish appear to grow at an average rate. Juvenile growth rates derived from length frequencies for other sciaenid fishes were similar to our estimates for weakfish: *C. arenarius* (~1 mm/day, Shlossman and Chittenden 1981), *C. nothus* (0.8–1.3 mm/day, DeVries and Chittenden 1982). Shenker and Olla (1986) provide estimates of juvenile fish growth rates ranging from a low of 0.26 mm/day (*Sebastes melanops*) to a high of 4.7 mm/day (*Coryphaena hipporus*). Other growth rate estimates of juvenile fishes include: 1.5 mm/day for *Anoplopoma fimbria* (Boehlert and Yoklavich 1985), 1.0–1.3 mm/day for *Chanos chanos* (Kumagai et al. 1985), and 1.1 mm/day for *Alosa sapidissima* (Crecco and Savoy 1985).

The ecological advantage of extended spawnings that result in multiple cohorts within a single age-0 year-class can be thought of as a "hedged bet" strategy that spreads age-0 production over time to take advantage of a variable environment (Lambert and Ware 1984). However, distinct cohorts within age-0 fish can also result from environmental factors acting on a single spawning effort; for example, through variation in prey availability (Timmons et al. 1980, Keast and Eadie 1985, Wicker and Johnson 1987), or a combination of biotic and abiotic factors (Lambert 1984, Crecco and Savoy 1985). However, previously published information indicates that the multiple cohorts observed in the present study probably resulted from multiple spawnings. Shepherd and Grimes (1984) showed that large weakfish "tiderunners" 55–80 cm enter the Delaware Bay estuary in the spring and spawn. In the summer these were replaced by 25–35 cm gravid weakfish. Harmic (1958) showed a repeating pattern of multiple spawning over 3 years, where a peak of egg abundance occurred in mid-June, followed by a conspicuous gap, and another peak in mid-July.

In summary, the present study showed that multiple cohorts exist within the age-0 year-class of Chesapeake Bay-York River weakfish. These cohorts showed significant differences in growth rates and appeared to partition habitats. Consequently, population studies directed at predicting year-class strength from juvenile surveys need to consider the potential for age-0 cohort variability.

Acknowledgments

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Abstract.—Over 6000 male snow crabs were tagged during a 6-year period in Conception Bay, Newfoundland, in order to estimate the increase in size at the time of molting. Ninety-two animals were recaptured which had usable information on growth increments. Based on the amount of growth, we hypothesized that 20 of these had molted once while the remainder molted twice. Two lines of evidence support this interpretation. First, animals in the group presumed to have molted twice were at liberty on average twice as long as those presumed to have molted once. Second, a regression line fitted to data on single-molters predicted the size after two molts in close agreement with a regression line fitted to data on double-molters. A nonlinear regression model was developed to estimate the parameters of the relationship between post- and pre-molt sizes using the combined data set for single and double molters. The method was also generalized to account for a quadratic relationship between post- and pre-molt size. For crabs in the size range 80–110 mm carapace width, the predicted size after molting in mm is equal to $7.398 + 1.038 \times$ pre-molt size. A similar study conducted in Bonavista Bay, Newfoundland, yielded growth information for 18 animals. The molt increments appear similar to those observed from Conception Bay.

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Growth per Molt of Male Snow Crab *Chionoecetes opilio* from Conception and Bonavista Bays, Newfoundland

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The snow crab *Chionoecetes opilio* has supported extensive commercial fisheries on both the Atlantic and Pacific coasts of North America since the 1960s (Elner and Bailey 1986). Snow crabs are also commercially exploited in Japan. Only the males are harvested in North America because females never attain commercially acceptable sizes. Efforts to manage the resources have been hampered by a lack of detailed life-history information. This is because the crabs are found in deep water (50–700 m) and are thus difficult to study.

Information on growth of snow crabs is required for effective management for at least three reasons: (1) for incorporation in a yield-per-recruit model, (2) to forecast the biomass available to the fishery from size-specific, pre-season biomass estimates, and (3) to interpret size-frequency distributions. Although growth can be studied in the laboratory, there is no guarantee that the observed growth will reflect what happens in free-living populations. Consequently, there is a need to estimate growth parameters from field data.

There have been some tagging studies of snow crab growth, but the reported results were either of a preliminary nature or were unsatisfactory due to tag retention problems (McBride 1982, Taylor 1982, Bailey and Dufour 1987). Improvements in tagging methods (Hurley et al. In press) have made field studies feasible.

Growth of crustacea is often estimated by studying two components: the increase in size at the time of molting (molt increment) and the timing of molting (either the intermolt period or the proportion molting in a given season). Recent work by Moriyasu and Mallet (1986) and O'Halloran and O'Dor (1988) has provided a method for estimating the proportion of the population that will molt in a given time period. In this paper, we concentrate on the problem of estimating the size-specific molt increment of snow crabs in Conception and Bonavista Bays, Newfoundland, from mark-recapture data consisting of the size at the time of tagging, the size at recapture, and the time at liberty.

Conception and Bonavista Bays are deepwater bays on the Northeast coast of Newfoundland (maximum depth 295 m in Conception Bay; 412 m in Bonavista Bay). Commercial fishing grounds for crabs exist at depths exceeding 180 m. The bottom type in these areas is predominantly mud or muddy sand with mean bottom temperatures ranging from -1.3 to $0.5°C$. Since the mid 1970s both areas have experienced high levels of commercial crab fishing effort (Taylor and O'Keefe 1987). While aggregations of crabs may be found at depths <180 m, the deeper commercial fishing grounds appear to have the soft substrate necessary for snow crab molting.

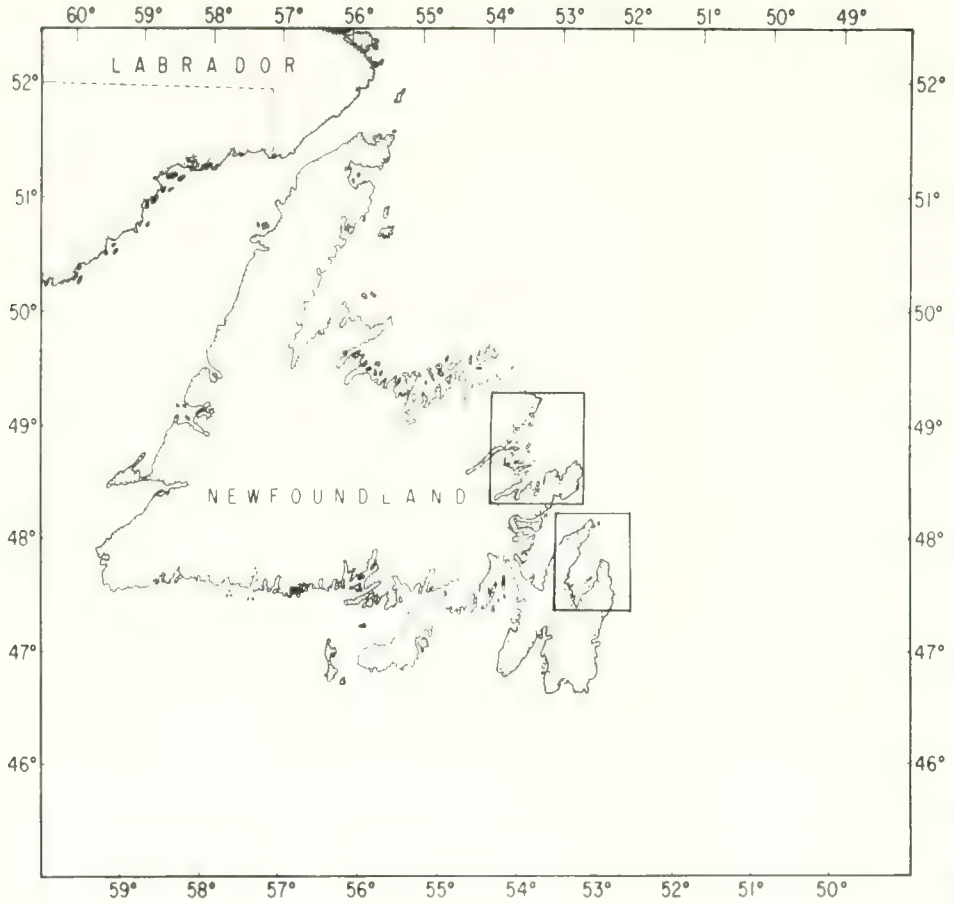

Figure 1
Map of Newfoundland, Canada, showing the location of Conception Bay (lower box) and Bonavista Bay (upper box).

Materials and methods

From 1979 to 1984, nine research cruises were made to Conception Bay, Newfoundland, Canada (47°30′N, 53°W, Fig. 1), to tag 6296 male snow crabs, size range 56–135 mm carapace width (CW). An additional 2253 male crabs, size range 45–125 mm CW, were tagged during four cruises to Bonavista Bay, Newfoundland (48°50′N, 53°20′W), from 1979 to 1984.

Crabs were captured using Japanese-style conical traps baited with squid *Illex illecebrosus* and set in longlines of twelve traps at depths ranging from 110 to 285 m. Traps were hauled after soaking for 24 hours.

Tagging was conducted in a manner designed to minimize mortality. Traps were spaced approximately 40 m apart, which allowed us to tag crabs from the trap on deck while the other traps remained in the water. Before tagging, we examined each animal and discarded any that appeared injured. Carapace width was measured to the nearest millimeter using vernier calipers. Animals were tagged with a T-bar tag (Floy Tag Mfg. Co., Inc., Seattle, WA 98105) and immediately released on location. Details of the tagging procedure are described in Hurley et al. (In press). Tags were inserted in the posterior ecdysial suture (epimeral line) which was made visible by applying gentle upward pressure to the carapace. The tagging location was 2–6 mm from the right coxopodite of the last walking leg. Before releasing the crab, the end of the tag was given a gentle tug. If the tag appeared loose, it was removed and the animal was discarded. To determine measurement errors, one biologist measured 90 animals three times in blind trials. The animals ranged in size from 63 to 124 mm. Recaptured animals were obtained mostly from commercial fishermen. Only animals that were examined by a staff biologist were used in the analysis.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results and discussion

Repeated measurements by a biologist of a group of crabs were always within 1 mm of the mean for each animal. Workers studying other species of large crustacea have suggested that measurements can be

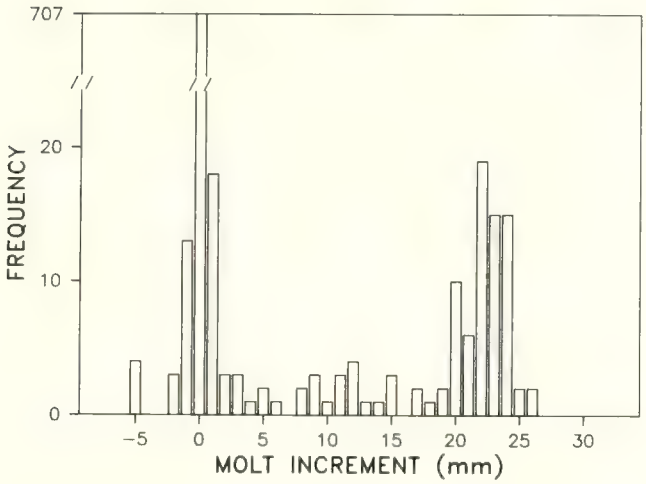

Figure 2

Frequency of occurrence of growth increments for recaptures of *Chionoecetes opilio* from Conception Bay.

precise to within 3 mm (Restrepo 1989, Hunt and Lyons 1986, Little 1972). If measurement errors occur at both the time of tagging and the time of recapture, then errors as large as 5 or 6 mm might be encountered.

Conception Bay

We recovered 850 tagged animals from Conception Bay. Of these, 751 had measured increases in size of 3 mm or less; three had increases of 4–5 mm; the remaining 93 animals had increases of at least 6 mm (Fig. 2). None of the three animals with molt increments of 4 or 5 mm were particularly small (premolt sizes: 92, 96, 99 mm). Consequently, these animals would not be expected to have particularly small increments. Their times at liberty were 325, 187, and 157 days, respectively. We assume that the 93 animals with increments of 6 mm or more molted at least once, and none of the other animals molted. The average time at liberty for animals which did not molt is under a year ($\bar{x}$ 322 days, median 251 days, range 6–1598 days; Fig. 3).

The size at recapture of Conception Bay crabs which molted was plotted against the size at tagging, and two distinct linear clouds of points were apparent (Fig. 4). The line indicating a 17% increase in size appears to separate the two clouds nicely. A reasonable working hypothesis is that the lower cloud consists of animals which molted once, while the upper cloud consists of animals which molted twice. One animal in the two-molt group was at liberty for only 29 days and was tagged and recaptured in a hard-shelled condition. Animals remain soft-shelled for 2–3 months after molting, and soft-shelled animals cannot molt (Taylor et al. 1989).

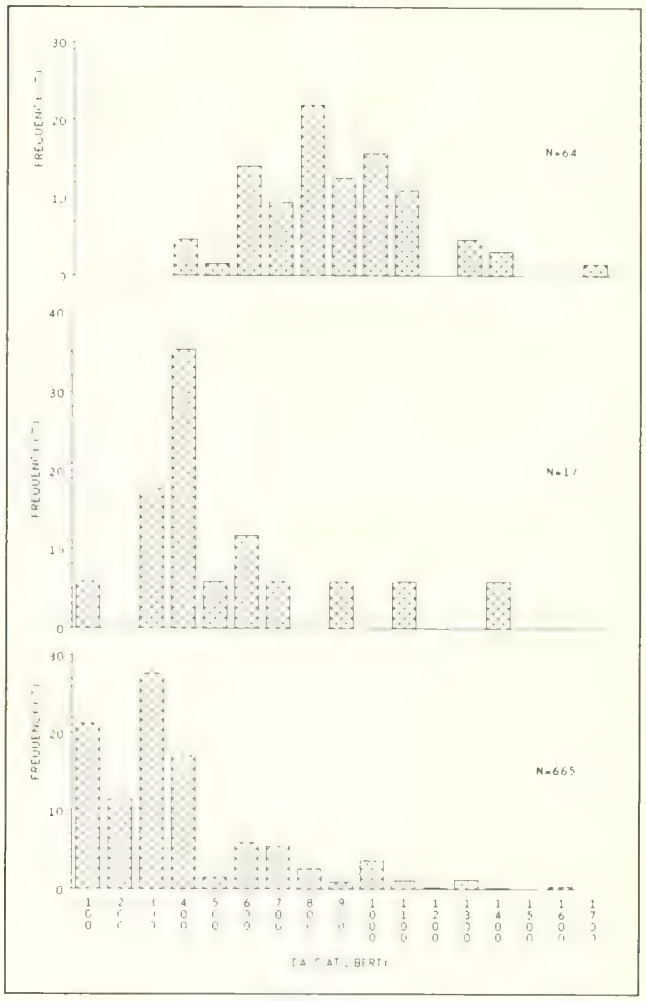

Figure 3

Histograms of times at liberty for Conception Bay *Chionoecetes opilio*. Upper figure corresponds to the upper cloud of points in Figure 4, i.e., to animals believed to have molted twice. Middle figure corresponds to the lower cloud in Figure 4. Lower figure corresponds to recaptured animals which had not molted while at liberty.

For this reason, this animal was eliminated from further consideration.

The times at liberty for 81 of the 92 Conception Bay animals which molted ranged from 18 to 1618 days. (Exact times at liberty could not be determined for 11 animals.) However, the mean time at liberty for the hypothesized two-molter group was approximately twice as long as for the single-molter group (828 vs. 468 days) and there was little overlap in the distributions of time at liberty for the two groups (Fig. 3). Animals which did not molt were at liberty for an average of 322 days. Although there is little information in the literature on intermolt periods for snow crabs, it is believed that crabs approaching commercial size molt once per year (Robichaud et al. 1989) and

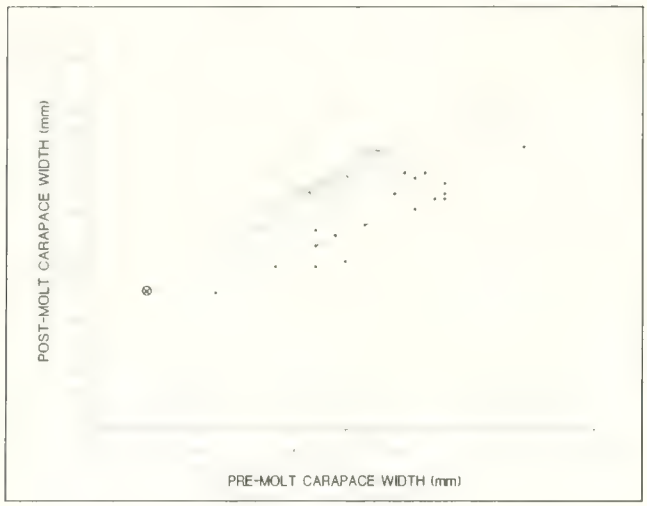

Figure 4

Plot of size at recapture vs. size at tagging for recaptures of *Chionoecetes opilio* from Conception Bay. The solid line, which indicates a 17% increase in size while at liberty, seems to separate the data into two clouds of points. Solid symbols represent animals believed to have molted once; open symbols represent animals which molted twice. Bulls-eye symbol represents one animal which was reportedly at liberty for only 29 days and which consequently was excluded from analysis.

Table 1

Regressions of length at recapture vs. length at tagging for the two groups of *Chionoecetes opilio* from Conception Bay shown in Figure 4. Lower cloud animals are presumed to have molted once; upper cloud, twice. Parameter estimates a and b pertain to equations (1) and (2) in the text.

Attribute	Lower cloud	Upper cloud
Number of observations	20	72
Adjusted r^2	0.85	0.92
Intercept (standard error)	17.250 (8.935)	12.667 (3.640)
Slope (standard error)	0.941 (0.091)	1.104 (0.039)
Interpretation of intercept	a	$a(1 + b)$
Interpretation of slope	b	b^2
a	17.250	6.179
b	0.941	1.051

that the largest crabs may skip a year between molts. Thus, the information on time at liberty supports the hypothesis that animals in the lower group of Figure 4 molted once while those in the upper group molted twice.

The data in the lower group in Figure 4 appear to be well described by a linear relationship:

$$\text{Recapture size} = a + b\,(\text{size at tagging}) + e \qquad (1)$$

where e is a random error term. Suppose that equation (1) describes the size after one molt. Then the size after two molts would be given by the recursive formula (Kurata 1962):

$$\text{Size after two molts} = a + b\,(a + b\,(\text{size at tagging})) + e. \qquad (2)$$

Application of equation (2) to the size at tagging should provide a good prediction of the size at recapture for animals in the upper group if the assumption is correct that equation (1) describes the size after one molt.

We fitted lines to the two clouds of points in Figure 4 by ordinary least squares (Table 1). The results are consistent with the hypothesis of one and two molts for the two groups. For example, the fitted equation (1) (with parameters estimated from the lower cloud of points) predicts that an animal 80 mm in size will be 92.53 mm after one molt. Inserting this estimate of 92.53 mm into equation (1) gives a predicted size of 104.32 mm after another molt. In contrast, a linear regression fitted to the upper cloud of points predicts that an animal 80 mm in size will be 100.91 mm after two molts, i.e., 3.41 mm smaller than the estimate from equation (1). Similarly, the size after two molts predicted by equation (1) for a 110-mm CW animal is 130.89 mm, whereas the size predicted by the regression for the upper cloud is 134.00 mm, i.e., 3.11 mm larger. Over the range of sizes for which we have data, results from the two equations agree closely. In fact, approximate confidence bands for the size after two molts, as determined from the lower regression line, enclose the confidence bands for the upper regression line over the entire range of the data (Fig. 5; see Appendix A for derivation of approximate confidence bands). We therefore conclude that animals in the lower cloud of points molted once, while those in the upper cloud molted twice.

The regressions in Table 1 are based on 20 and 72 animals. Since the sample sizes are small, it would be useful to use the combined molting data from all 92 animals to derive a best estimate of the parameters a and b. This can be accomplished by combining equations (1) and (2) into a single equation in the form of a nonlinear regression model. Let Y be the observed size at the time of recovery, X be the size at tagging, and let Z be an indicator variable for whether an animal molted once or twice, i.e., let

$$Z = \begin{cases} 0, \text{ animal molted once} \\ 1, \text{ animal molted twice.} \end{cases}$$

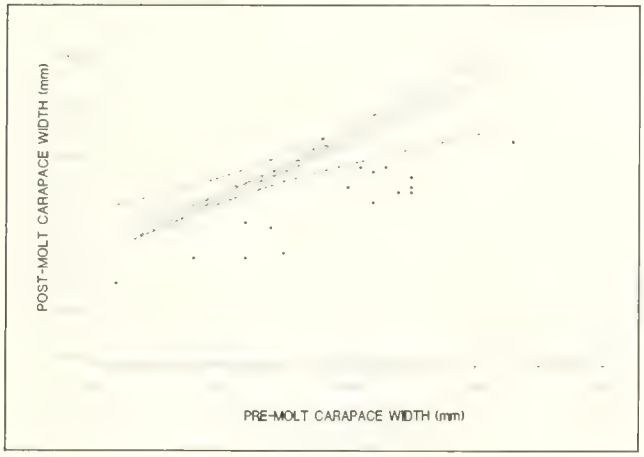

Figure 5

Recapture data for *Chionoecetes opilio* from Conception Bay. Solid symbols represent animals presumed to have molted once; open symbols represent animals which molted twice. Solid lines show the 95% confidence band obtained from the linear regression fitted to the open circle data. Dashed lines give an approximate 95% confidence band for the size after two molts based on the regression for the presumed single-molters (solid symbols). (See Appendix A for method of constructing the confidence band.) The dashed lines enclose the solid lines, indicating that the two predictions of size after two molts are not significantly different. This supports the idea that the two clouds in Figure 3 represent single- and double-molters.

Table 2

Estimates of the parameters a and b in the nonlinear regression model relating size at recapture (Y) of Conception Bay *Chionoecetes opilio* to size at tagging (X) for animals molting once or twice. The model is: $Y = a + abZ + bX + b(b - 1)ZX + e$, where e is the error term and $Z = 0$ if the animal molted once, and 1 if the animal molted twice.

Parameter	Estimate	Standard error	
a	7.398	2.074	correlation
b	1.038	0.021	−0.998

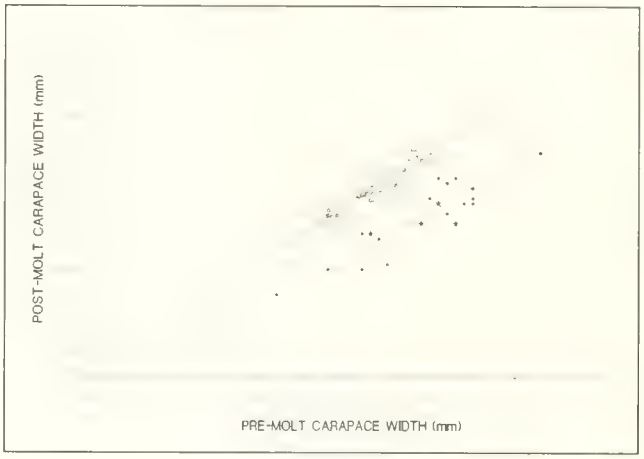

Figure 6

Plot of size at recapture vs. size at tagging for recaptures of *Chionoecetes opilio* from Conception Bay (circles) and Bonavista Bay (triangles and stars). Solid circles and stars represent animals believed to have molted once; open triangles and circles represent animals which molted twice. Diamond represents an animal from Bonavista Bay at liberty for ~1000 days which was presumed to have molted three or more times. Large circle represents an animal which normally would be assumed to have molted twice; however, it was reportedly at liberty for only 29 days and consequently was excluded from analysis. Regression lines were determined using equation (3) from all data on single and double molters from both bays.

Then the growth parameters a and b can be estimated by regressing Y on X and Z in the regression model

$$Y = a + abZ + bX + b(b - 1)ZX + e \qquad (3)$$

where e is a random error term. Equation (3) reduces to (1) when $Z = 0$ and to (2) when $Z = 1$. The model is generalized in Appendix B to account for a quadratic relationship between post- and pre-molt size. The predicted sizes from the fitted equation (3) (Table 2) are very similar to the results obtained using equations (1) and (2) separately.

Bonavista Bay

Molt information was obtained from 18 animals recaptured in Bonavista Bay. Of these, four animals appeared to have molted once; 13 animals appeared to have molted twice; and one animal at liberty for approximately 1000 days appeared to have molted three or more times (Fig. 6). This interpretation is supported by the fact that the animals presumed to have molted once were at liberty for an average of 198 days, while the animals presumed to have molted twice were at liberty for an average of 698 days.

The molt increments appeared very similar to those from Conception Bay. Since there is not much information from Bonavista Bay, we computed a regression to predict molt increments for Bonavista Bay crabs using the combined recapture data on single and double molters from Bonavista and Conception Bays. The predicted size after molting is given by

$$\text{Predicted size} = 9.21 + 1.02\ (\text{pre-molt size}).$$

Other populations

The predicted molt increments from equation (3) for Conception Bay crabs (Table 2) were very close to a constant (10.5 – 11.7 mm) over the size range of animals we studied (82–113 mm CW). These estimates are

consistent with the limited information from a tagging study in the Gulf of Alaska. McBride (1982) reported the mean growth increment of six tagged snow crabs at liberty for up to 1 year was 14.7 mm. McBride's animals were somewhat larger than those in our study ($\bar{x}$ 113.8 mm, range 108–124 mm CW at tagging) and would, on the basis of our regression, be predicted to have slightly larger molt increments.

Laboratory studies of snow crab growth are also consistent with our findings. O'Halloran (1985) reported an average molt increment of 11.6 mm for eight animals. However, five of the eight animals had their eyestalks ablated bilaterally and these animals died during ecdysis. Consequently, these estimates are not very reliable. Miller and Watson (1976) and R.J. Miller (Dep. Fish. Oceans, Halifax, Nova Scotia, Canada 83J 2S7, pers. commun., June 1989) observed a mean molt increment of 15.5 mm for 18 crabs ranging in pre-molt size from 59.3 to 101.1 mm CW ($\bar{x}$ 80.5 mm). G. Hurley (Hurley Fish. Consulting, 45 Alderney Dr., Dartmouth, Nova Scotia, Canada B2Y 2N6, pers. commun., June 1989) observed a mean increment of 13.9 mm for 47 crabs, size range 60.7–83.4 mm CW ($\bar{x}$ 66.1 mm). In these studies, crabs were fed *ad libitum*. In another laboratory study, Moriyasu et al. (1987) reported a regression line that indicates that animals in the size range we studied (82–113 mm CW) have predicted molt increments of 14–16 mm CW.

Molt increments have also been estimated by size-frequency analysis for Japanese populations of snow crabs. Kon et al. (1968) reported estimates for small individuals. Ito (1970) suggested that 81-mm CW individuals molt to 97 mm, then to 111 mm and 121 mm (i.e., molt increments of 16, 14, and 10 mm). Kon (1980) suggested that 80-mm CW individuals molt to 93.4 mm, then to 105.6 and 116.7 mm (molt increments of 13.4, 12.2, and 11.1 mm). These estimates are similar to the ones we derived from the tagging data. Robichaud et al. (1989) analyzed size-frequency distributions of snow crabs from the Gulf of St. Lawrence. Their samples consisted of small animals, so their results are not comparable to the results presented here.

Effect of possible terminal molt

Some workers believe that male snow crabs undergo a "terminal" or final molt which is associated with a change in allometry. Although this idea is controversial (see Jamieson and McKone 1988 for reviews), it is worth examining whether the two groups evident in Figure 4 might reasonably be interpreted as those molting to the terminal state (e.g., lower group) and those molting but not to the terminal state (upper group). To accept this hypothesis implies that all of the following are accepted:

(1) males do, in fact, undergo a terminal molt;

(2) the size increment at the terminal molt is considerably different (presumably smaller) than the penultimate molt increment;

(3) it is a coincidence that the animals in the upper group were at liberty twice as long as those in the lower group (828 vs. 468 days on average), and that the animals which did not molt were at liberty for less than a year on average ($\bar{x}$ 322 days);

(4) it is a coincidence that the size predicted after two molts by the regression fitted to the lower cloud of points is in close agreement to the size after two molts predicted by the regression fitted to the upper cloud of points;

(5) there must be an as yet unidentified reason why a third cloud of points, corresponding to animals which molted twice, is not evident in Figure 4.

Even if males undergo a terminal molt, there is no evidence to suggest that the final molt increment is distinctly smaller than the penultimate molt increment. In an aquarium study, Moriyasu et al. (1987) found, for male snow crabs in the size range 60–70 mm CW, that animals molting to the large-clawed state have molt increments about 3 mm smaller than those molting to a small-clawed state. This small difference in molt increments is not sufficient to account for the two clouds we identified in the field observations. Ennis et al. (1988) have shown that males can become functionally mature before attaining the morphometry associated with the terminal molt. Hence, the terminal molt is not necessarily associated with a diversion of energy from growth to reproductive processes, and the terminal molt increment need not be small. We conclude that if animals undergo a terminal molt, the molt increment at this time is similar to the penultimate molt increment. We do not rule out the possibility that some of the scatter about the regressions through the two clouds of points is due to mixing terminal and non-terminal molt data.

In summary, our interpretation of the tagging data is supported by two lines of evidence. Animals presumed to have molted twice were at liberty twice as long on average as animals presumed to have molted once. Also, the predicted size after two molts, as estimated from data on animals presumed to have molted once, agrees closely with the predicted size estimated from data on animals presumed to have molted twice. We conclude that male snow crabs in the size range 75–115 mm have molt increments of around 11 mm. Our results are consistent with the limited information about snow crab growth in the literature.

Acknowledgments

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Appendix A
Derivation of Confidence Bands

The predicted size after one molt can be obtained by regressing the size at recapture on the size at tagging for those animals which molted once (text equation 1). Thus,

$$\text{predicted recapture size} = a + bX \qquad \text{(A.1)}$$

where a and b are parameter estimates and X is the size at tagging. Estimates of the variances and covariances (i.e., $V(a)$, $V(b)$, $Cov(a,b)$) are easily obtained in the standard way.

The predicted size after two molts is obtained from A.1 as

$$Y = \text{predicted size after two months}$$
$$= a + b(a + bX) = a + ab + b^2X.$$

An approximate (asymptotic) estimate of the variance of the size after two months, V(Y), is found by the Taylor's series or delta method to be

$$V(Y) = \left(\frac{\partial Y}{\partial a}\right)^2 V(a) + \left(\frac{\partial Y}{\partial b}\right)^2 V(b)$$
$$+ 2\left(\frac{\partial Y}{\partial a}\right)\left(\frac{\partial Y}{\partial b}\right) Cov(a,b)$$

where the derivatives are evaluated at the parameter estimates. Thus.

$$V(Y) = (1 + b)^2 V(a) + (a + 2bx)^2 V(b)$$
$$2(1 + b)(a + 2bx) Cov(a,b).$$

An approximate 95% confidence band is thus obtained as

$$Y \pm 2\sqrt{V(Y)}.$$

Appendix B Estimating molt increments for a quadratic model

Over the size range of animals we studied, the relationship between post- and pre-molt size appeared linear. However, when a wide range of pre-molt sizes is considered, it is common to find a curvilinear relationship which may be modeled satisfactorily by a quadratic equation. The non-linear regression model (equation 3) in the text can be generalized to allow estimation for the quadratic model.

Let the size at tagging be denoted by X, and assume the size after one molt is given by

$$\text{size after one molt} = a + bX + cX^2. \qquad \text{(B.1)}$$

Then the size after two molts is given by

$$\text{size after 2 molts} = a + b(a + bX + cX^2)$$
$$+ c(a + bX + cX^2)^2. \qquad \text{(B.2)}$$

As before, let Y be the size at recapture (for animals molting once or twice), and define Z to be an indicator variable for whether an animal molted once or twice, i.e., let

$$Z = \begin{cases} 0, \text{ animal molted once} \\ 1, \text{ animal molted twice} \end{cases}$$

Then equations (B.1) and (B.2) can be combined in a single non-linear regression as

$$Y = a + (ab + a^2c)Z + bX + b(b - 1 + 2ac)ZX$$
$$+ c^2X + c(b + 2ac + b^2 - 1)ZX^2$$
$$+ 2bc^2ZX^3 + c^3ZX^4 + e \qquad \text{(B.3)}$$

where e is the random error term. Equation (B.3) reduces to (B.1) when $Z = 0$ and to (B.2) when $Z = 1$.

Abstract.– We applied Shepherd's length composition analysis (SRLCA) to research trawl survey catches of Gulf of Maine northern shrimp *Pandalus borealis* to test the efficiency of the method in interpreting the age structure of a length-frequency distribution incorporating significant variation in growth and recruitment rates. We evaluated the performance of the method by comparing the von Bertalanffy growth parameters provided by SRLCA and subsequently derived age frequencies and instantaneous total mortality rates with previously accepted results based on simple visual inspection of the annual length-frequency distributions.

In spite of the variable growth and recruitment rates exhibited by the stock, SRLCA yielded information providing a resolution of the length-frequency data close to *a priori* assumptions, although information external to the procedure was needed to select the best interpretation from among several locally optimal solutions.

A Practical Assessment of the Performance of Shepherd's Length Composition Analysis (SRLCA): Application to Gulf of Maine Northern Shrimp *Pandalus borealis* Survey Data

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The analysis of length-frequency modes was the first method used by aquatic biologists to delineate successive cohorts in fish and invertebrate populations. Simple visual inspection of modes was developed first (e.g., the "Petersen" method [Petersen 1891]); this relies heavily on the intuition of the scientist for the correct separation of age groups. Later workers assumed a normal distribution underlying the observed length modes, and graphical methods using normal probability paper were used to resolve length distributions to cohorts by the successive identification and removal of suspected age groups. The method of Cassie (1954) is probably the best known of these graphical procedures, which rely to a large degree on subjective decisions of the scientist. Difficulty in defining modes for older age groups, problems in interpretation caused by variable growth rates and recruitment, and an inability to reproduce the interpretation of age groups from one worker to the next have limited the utility of these simple methods.

For most finfish stocks, the interpretation of growth intervals on hard body parts (e.g., scales, otoliths, spines, and vertebrae) has evolved as the ageing method of choice, replacing length-composition analysis methods. For many taxa, however, the interpretation of growth intervals from age structures is difficult, either due to problems in identifying periodic marks or because of the lack of suitable hard structure. For fast-growing, short-lived tropical finfish, and invertebrates such as lobsters, crabs, shrimps, and squids, the resolution to ages of modes in length-frequency distributions continues to be the primary method used to estimate growth and age structure of populations. Recently developed methods directed to interpreting length-frequency distributions generally fall into two categories. The first group treats the problem as one of statistically resolving a mixture of distributions, and usually assumes an underlying normal distribution for the components. The parameters resulting in the best match between the area under the theoretical distribution and the area under the observed length distribution are selected by employing chi-square or maximum likelihood methods. These distribution mixture methods require some prior constraint on the number of length modes and the bounds of the parameters to prevent biologically unrealistic results. The lineage of this approach includes the methods of Hasselblad (1966), Tomlinson (computer program

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NORMSEP; 1971), Yong and Skillman (computer program ENORMSEP; 1975), McNew and Summerfelt (1978), and MacDonald and Pitcher (computer program MIX; 1979). The distribution mixture method of Schnute and Fournier (1980) uses a growth model to impose these constraints. A second category of procedures assumes a specific growth function (usually the von Bertalanffy) and attempts to match predicted length modes to those observed. Among these methods are the ELEFAN I procedure of Pauly and David (1981), and Shepherd's length composition analysis (1987).

The Shepherd length composition analysis method (SRLCA) (Shepherd 1987) relies on a goodness-of-fit score function which varies according to the correspondence of observed and predicted length-frequency modes for given pairs of von Bertalanffy growth parameters (L_{inf} and K), thus presumably constraining the indication of optimal parameters to within biologically realistic bounds. SRLCA has fewer subjective input requirements than the distribution mixture methods (Shepherd 1987). Basson et al. (1988) performed Monte Carlo tests of SRLCA and noted that although SRLCA provided biased results for simulated data with large variation in length-at-age, SRLCA generally performed better than ELEFAN I.

To test the performance of SRLCA on an observed, potentially difficult-to-interpret data set, as suggested by Shepherd (1987), we applied a version of SRLCA using the von Bertalanffy growth equation to research trawl survey data for Gulf of Maine northern shrimp *Pandalus borealis*, and compared our results with accepted interpretations of the data. Currently, simple visual inspection and information on sexual characteristics are used to resolve survey length frequency to age frequency, providing subsequent estimates of relative adult stock abundance, recruitment success, and total instantaneous mortality rates (Z) (McInnes 1986, NSTC 1987). Survey results reveal that this stock has experienced variable recruitment and growth during 1982 to 1988 (NSTC 1984, 1985, 1986, 1987, 1988). Although true ages for northern shrimp are not available for use as "ground truth" in this evaluation of SRLCA performance, we feel our assessment of the method is valuable since it is based on application to real data of the type which in practice might require the use of length-based assessment methodology.

Methods

Analysis

SRLCA compares the observed length-frequency distribution with that expected from the von Bertalanffy equation for given test pairs of L_{inf} and K by application of a continuous, periodic test function of the form:

$$T_i = (\{\sin \pi \{t_{max} - t_{min}\}\} / \{\pi \{t_{max} - t_{min}\}\}) \times (\cos 2\pi [t_{bar} - t_s])$$

where T_i is the value of the function for a given length interval i, t_{max} and t_{min} are ages at the upper and lower bounds of the interval for a given test set of growth parameters, t_{bar} is the average of t_{max} and t_{min}, and t_s is the date of observation, expressed as a fractional part of the age (e.g, annual) cycle (Shepherd 1987).

A measure of goodness-of-fit is then used to determine the best fitting set of growth parameters for the observed length-frequency distribution. This measure, the score function S, is given by:

$$S = \sum_i T_i N_i^{1/2}$$

where i indexes the length intervals, T is as indicated previously, and N is the number of animals in each interval. Taking the square root of N helps reduce the sensitivity of the score function to unusually large numbers of animals in a given length interval (e.g., in the event of exceptional recruitment; Shepherd 1987). Cumulative scores are large and positive when length modes predicted for a given pair of growth parameters are consistent with observed length-frequency modes, with negative scores indicating inconsistency. Shepherd (1987) suggested that regions of nearly constant scores within the K by L_{inf} score matrix may provide an indication of the shape of the confidence interval around pairs of parameters (e.g., Shepherd suggests a region equal to one-half of the maximum score might approximate the 95% confidence interval). Typically, several regions (hereafter called ridges) of high scores will be observed for each length-frequency distribution analyzed, with local maxima in each ridge that provide alternative interpretations of the data.

Length-frequency data

Gulf of Maine northern shrimp are protandric hermaphrodites, with the females the target of a valuable winter/spring fishery in the western Gulf of Maine (see McInnes 1986 for an overview of the fishery). A research vessel trawl survey was implemented in 1983 to provide a fisheries-independent source of data for the stock. A stratified random trawl survey is conducted annually during late July through mid-August aboard the Northeast Fisheries Center (NEFC) RV *Gloria Michelle* in the western Gulf of Maine (Fig. 1).

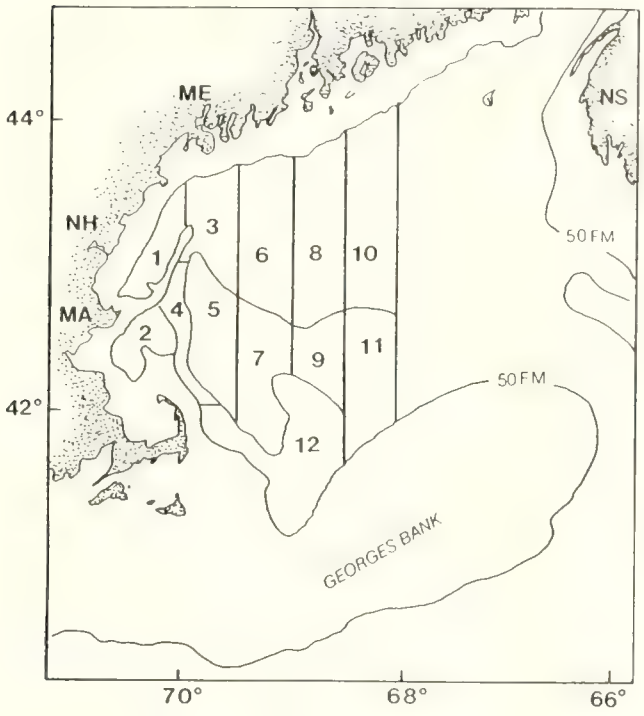

Figure 1

Western Gulf of Maine region with major bathymetric features and 50-fathom (100-m) isobath. Northern shrimp survey area extends from 68°W longitude to the 50-fathom isobath, except for stratum 2, where the sampled area extends to the 30-fathom (60-m) isobath.

Length-frequency data from identical sample strata sets (strata 1, 3, and 5–8) are available for 1984–88 (NSTC 1984, 1985, 1986, 1987, 1988). Trawl gear consists of a modified 4-seam commercial shrimp trawl with 35 mm (1.4 inch) stretched mesh in the body of the net and 32 mm (1.3 inch) stretched mesh in the extension and codend, with "rockhopper" ground gear to allow sampling over rough bottom (McInnes 1986). Samples (2 kg) of each tow are retained for length measurement and sex determination. All shrimp in the sample are measured, with mid-dorsal carapace lengths aggregated by 0.5-mm intervals (nearest 0.5 mm below that measured). A 1-kg subsample is retained for determination of sex and spawning stage.

To date, abundance and biomass indices from the RV *Gloria Michelle* survey (stratified mean number per tow, stratified mean weight [kg] per tow) have proven to be accurate predictors of year-class size and commercial fishery performance (total catch and catch-per-unit-effort; NSTC 1988). Coefficients of variation for stratified mean number and weight (kg) per tow, aggregated over all sample strata, have averaged (1984–88) about 13% and 12%, respectively, indicating relatively high precision.

A priori assumptions

Information is available from previous analyses of the Gulf of Maine northern shrimp length-frequency distributions to provide a baseline interpretation for evaluation of SRLCA results. The von Bertalanffy growth equation has been the accepted means of describing the growth of *P. borealis* (Frechette and Parsons 1983). For the Gulf of Maine stock, growth parameters were expected to be in the range of those previously estimated for this stock. These include (1) parameters derived here by nonlinear least-squares regression analysis of mean carapace length (CL) at age data summarized by Haynes and Wigley (1969; L_{inf} = 32 mm, K = 0.46, t_0 = −0.12), and (2) parameters derived from NEFC groundfish bottomtrawl survey data for northern shrimp (NEFC unpubl. data in McInnes 1986; L_{inf} = 35.2 mm, K = 0.36, t_0 = 0.06). In both of these studies, age was estimated by visual inspection of length-frequency distributions.

For Gulf of Maine northern shrimp survey data, a 1 March birthday was assumed (Apollonio et al. 1986), with an average catch date of 1 August (NSTC 1984, 1985, 1986, 1987, 1988); thus t_s was set equal to 0.42 for all SRLCA runs in this exercise. The usual presence of four age groups (ages 1–4) in the survey catch was suspected (McInnes 1986), with a maximum age of 5 years (Haynes and Wigley 1969, Apollonio et al. 1986), based on modes in length frequencies and sexual characteristics (Allen 1959, McCrary 1971). Northern shrimp in a length range of 13–18 mm CL are generally assumed to be of age-group 1, and mainly immature and mature males, while shrimp 18–22 mm CL are assumed to be age 2 and mostly mature males. Animals in the 22–25 mm CL interval are assumed age 3, usually females with no previous spawning history. Shrimp larger than 25 mm CL are assumed to be females of age-group 4, with possible age-group 5 female shrimp at CL greater than 29 mm. The survey samples northern shrimp in a CL range of 10–32 mm (Fig. 2), with animals assumed fully recruited to the gear at about 19–20 mm CL, or age 2 and older (Blott et al. 1983). Previous interpretations of survey results and commercial fishery performance suggest that the 1982 and 1987 year-classes (YC) of Gulf of Maine northern shrimp were strong, and the 1983 YC very weak, with the remaining cohorts (1984–86) of about equal strength (NSTC 1987, 1988).

Model evaluation

Exploratory runs were performed using L_{inf} values ranging from 20 to 50 mm, in 1-mm steps, and K values ranging from 0.20 to 0.50, in 0.01 steps, encompassing a very wide range of values (about ±50%) around

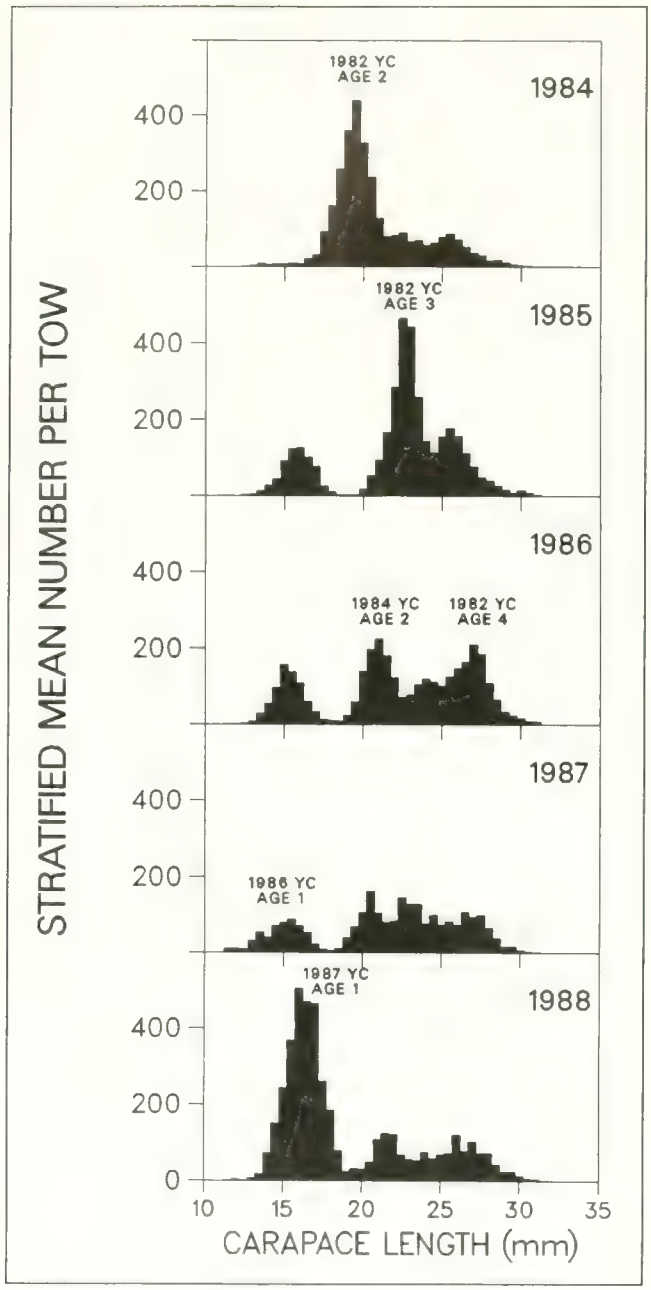

Figure 2

Length-frequency distributions (stratified mean number per tow) for *Pandalus borealis* collected in the western Gulf of Maine during the 1984–88 northern shrimp surveys aboard RV *Gloria Michelle*.

the growth parameters previously estimated for this stock of *P. borealis*, in order to adequately explore the high score ridges provided by the SRLCA score function. Preliminary evaluation of the highest scoring parameter values from each ridge, along with several local maxima (higher score than all eight nearest neighbors) within each ridge, indicated that parameter pairs within a given ridge tended to provide similar interpretations of the number of modes (assumed age groups) present in the observed length frequency, as expected from earlier testing of the method (Shepherd et al. 1987). Values of the optimum value of t_0 corresponding to K and L_{inf} parameter pairs are the decimal fraction part of t_0, and are indeterminate with respect to the addition or subtraction of any whole number of years (Shepherd 1987).

SRLCA results were examined in the context of previously developed parameter estimates and *a priori* assumptions, and alternative parameters were evaluated when the highest scoring values did not agree with prior interpretations of the number and position of modes (assumed age groups) expected. SRLCA was first applied to annual distributions independently, and then to distributions from 1984 to 1988 sequentially pooled in a single run. The annual distributions were analyzed primarily to evaluate interpretations provided by SRLCA given the variable patterns of growth and recruitment in the data. Growth parameters and subsequently resolved age frequencies from the final pooled analysis were used to estimate total mortality for comparison with rates estimated by visual resolution of the length-frequency data to age.

Shepherd (1987) noted that the number of older ages determined by decomposition of the length-frequency distribution according to the von Bertalanffy growth equation is dependent to a large degree on the value of L_{inf}, and suggested that parameters selected by SRLCA might be most appropriate for subsequent use in other length-based analyses, rather than to slice length frequencies to ages, unless additional data (e.g., knowledge of the expected number of cohorts) are available to select the ridge containing the "correct" parameter pair (see also Shepherd et al. 1987). In this exercise, we elected to proceed with resolution to cohorts, and subsequent age-based mortality estimation, both because of the apparently nonequilibrium nature of this northern shrimp population (thus limiting the utility of length-based methods which assume steady-state conditions), and to provide results comparable with those previously estimated (NSTC 1984, 1985, 1986, 1987, 1988).

Results

Annual length frequencies

1984 distribution This distribution is characterized by a dominant mode centered at 19.5 mm (Fig. 2). *A priori* interpretation suggested that the dominant mode at 19–20 mm should be age-group 2 shrimp (a strong 1982 YC), with shrimp 22–24 mm probably age-

Table 1

Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1984 northern shrimp survey length-frequency distribution: primary and secondary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	35	0.50	47.0
	40	0.43	63.9
	45	0.36	64.4
	50	0.30	62.7
	39	0.50	67.7[1]
	41	0.43	65.8[2]
Secondary ridge crest	35	0.42	41.4[1]
	40	0.30	37.4
	36	0.37	40.3 *

[1] High score parameters of ridge crest, on boundary of explored space.
[2] High score parameters of ridge crest, nonboundary maximum.
* Parameters selected for final evaluation.

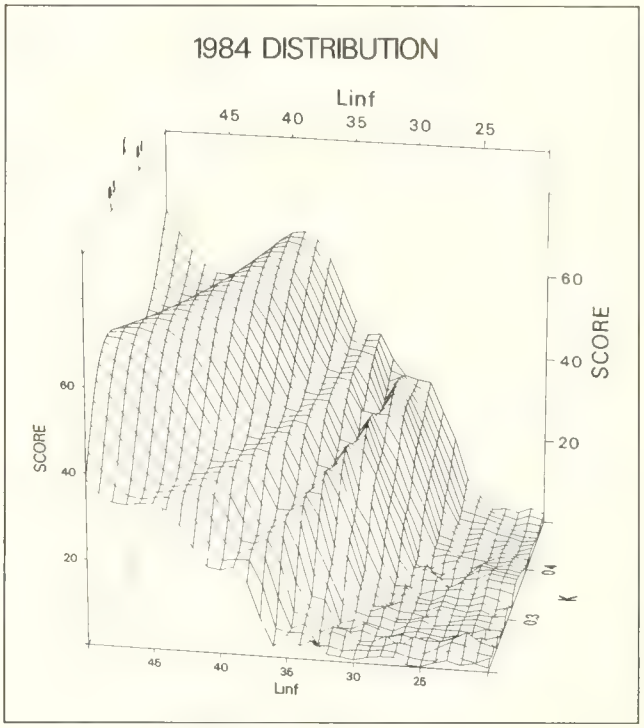

Figure 3

Response surface of the SRLCA score function for the northern shrimp survey 1984 length-frequency distribution.

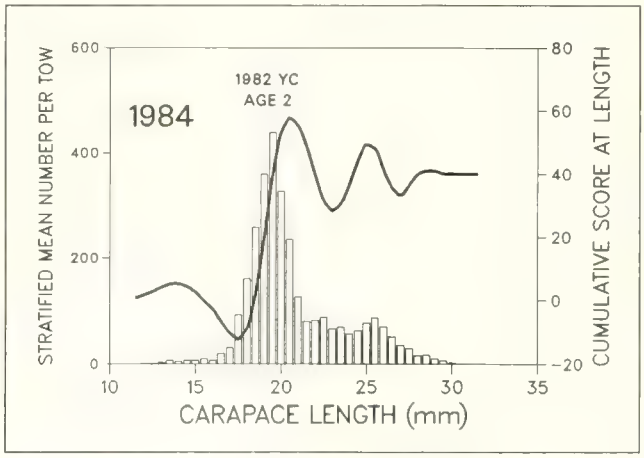

Figure 4

Northern shrimp survey 1984 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 36 mm, K = 0.37).

group 3, and animals >25 mm defined as age 4+ (NSTC 1984). SRLCA scores exhibited a broad, primary (highest scores) ridge of scores within the explored parameter space ranging from a high score on the border of explored parameter space at L_{inf} = 39 mm, K = 0.50 to L_{inf} = 50 mm, K = 0.30, with a nonboundary local maximum at L_{inf} = 41 mm, K = 0.43 (Table 1, Fig. 3). Based on parameters in this ridge, the length frequency was interpreted as a single dominant mode (age-group 1), with the distribution to the right of the mode classified as two older age-groups, for a total of three cohorts present. A secondary ridge of scores, from L_{inf} = 33 mm, K = 0.50 to L_{inf} = 38 mm, K = 0.30, with a nonboundary local maximum at L_{inf} = 36 mm, K = 0.37 (Table 1, Fig. 3), classified four ages and defined the dominant mode as age 2, but did not interpret the small modes at 22.5 and 25.5 mm in accordance with prior assumptions (assumed age groups 3 and 4, respectively). However, this secondary ridge most closely matched the *a priori* interpretation, and represented the best performance of SRLCA for the 1984 data (Fig. 4). A tertiary ridge (a spur of the secondary) ranged from a nonboundary maximum at L_{inf} = 31 mm, K = 0.46 to L_{inf} = 34 mm, K = 0.30, and interpreted the length frequency in nearly the same manner as parameters from the secondary ridge.

1985 distribution Previous work suggested that the first two modes of this distribution, 13–18 mm and 20–24 mm, should be interpreted as age groups 1 (1984 YC) and 3 (the strong 1982 YC), thus confronting SRLCA with a "missing cohort" situation (the weak 1983 YC; Fig. 2). Sex determinations further showed that shrimp in the 20–24 mm mode were not the expected first-year females, but mostly mature males that seemed not to have undergone transition during the previous winter (NSTC 1985). Inspection of the position of this age-3 mode, relative to the modal lengths

Table 2

Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1985 northern shrimp survey length-frequency distribution: primary, secondary, and tertiary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	35	0.48	85.2[2]
	40	0.34	82.6
	45	0.26	78.7
	50	0.21	75.2
Secondary ridge crest	42	0.50	63.0
	46	0.41	69.7
	50	0.34	74.1[1]
Tertiary ridge crest	28	0.50	29.0[1]
	30	0.37	23.6
	32	0.30	22.5
	34	0.27	21.4
	36	0.23	23.4
	38	0.20	23.8
	29	0.42	25.3 *

[1] High score parameters of ridge crest, on boundary of explored space.
[2] High score parameters of ridge crest, nonboundary maximum.
*Parameters selected for final evaluation.

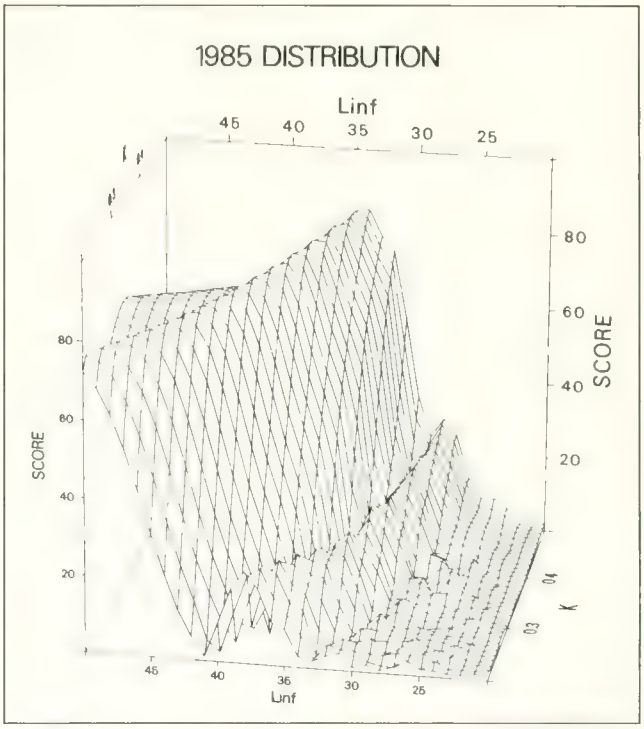

Figure 5

Response surface of the SRLCA score function for the northern shrimp survey 1985 length-frequency distribution.

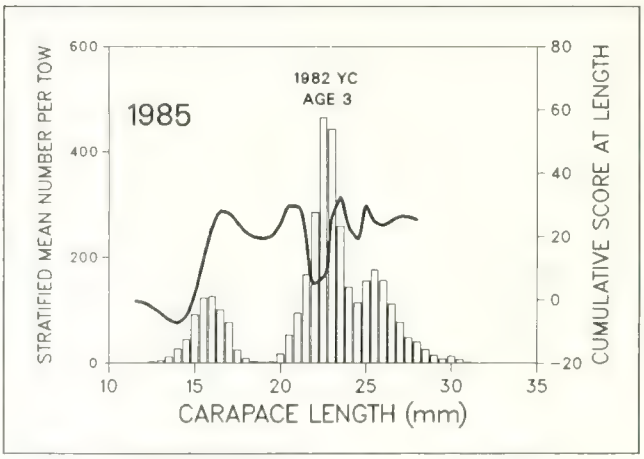

Figure 6

Northern shrimp survey 1985 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 29 mm, K = 0.42).

of assumed age-3 shrimp in the two subsequent years, suggests that the 1982 YC may also have experienced a slower growth rate between ages 2 and 3 than preceding cohorts.

The highest value in the SRLCA primary score ridge was at $L_{inf} = 35$ mm, $K = 0.48$, with the ridge then continuing to $L_{inf} = 50$ mm, $K = 0.21$. Parameters in this primary ridge classified the first two modes as successive cohorts, with three age groups total. A secondary ridge, from $L_{inf} = 42$ mm, $K = 0.50$ to a boundary maximum at $L_{inf} = 50$ mm, $K = 0.34$, resolved the distribution to only two age groups, with modal lengths of 17.0 and 26.5 mm for ages 1 and 2. It was necessary to explore a tertiary ridge, with a nonboundary local maximum at $L_{inf} = 29$ mm, $K = 0.42$, to successfully interpret the first two length modes as age groups 1 and 3, with shrimp >24.5 mm resolved to two main age-groups (Table 2; Fig. 5, 6).

1986 distribution This distribution is characterized by three clearly defined modes at 13–18 mm, 19–22 mm, and >25 mm, assumed to be ages 1, 2, and 4, and a small mode at 23 mm assumed to be either the 1983 cohort at age 3 or slow-growing shrimp from the 1982 cohort at age 4 (NSTC 1986; Fig. 2). Two ridges of comparable high scores were apparent from an initial SRLCA run, a primary ridge from $L_{inf} = 35$ mm, $K = 0.49$ to a boundary maximum at $L_{inf} = 50$ mm, $K = 0.22$, and a secondary ridge from $L_{inf} = 32$ mm, $K = 0.47$ to $L_{inf} = 40$ mm, $K = 0.23$ (Table 3, Fig. 7). The primary ridge identified three modal groups, matching the first observed mode well, but classifying shrimp between 18.5 and 24.5 mm as a single group, with the

Table 3

Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1986 northern shrimp survey length-frequency distribution: primary and secondary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	35	0.49	65.5
	40	0.34	74.1
	45	0.26	78.0
	50	0.22	79.9[1]
Secondary ridge crest	32	0.47	65.1
	34	0.37	65.6
	36	0.31	63.1
	38	0.27	59.9
	40	0.23	55.7
	33	0.42	66.1[2]*

[1] High score parameters of ridge crest, on boundary of explored space.
[2] High score parameters of ridge crest, nonboundary maximum.
*Parameters selected for final evaluation.

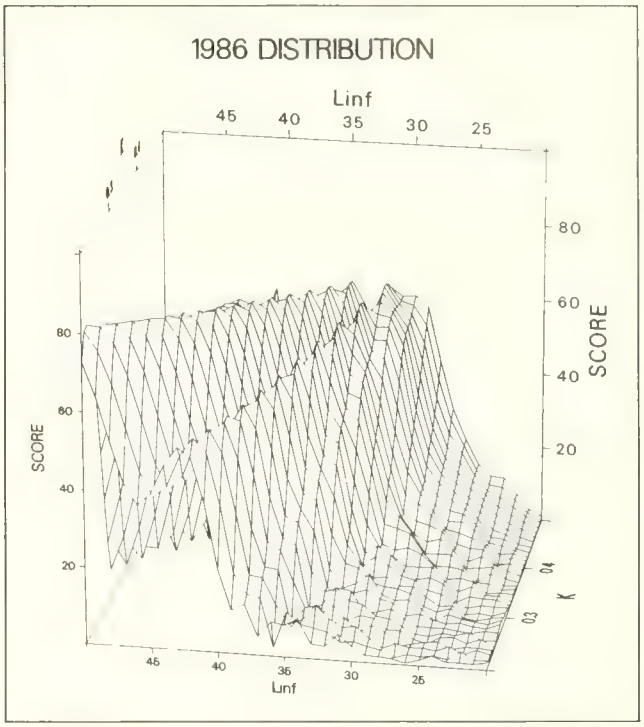

Figure 7

Response surface of the SRLCA score function for the northern shrimp survey 1986 length-frequency distribution.

last mode interpreted as age-3 shrimp. The secondary ridge high-score parameters classified the first, second, and fourth observed modes fairly well, with the highest scoring parameters (L_{inf} = 33 mm, K = 0.42) falling in an interval between previously estimated von Bertalanffy parameters. SRLCA was thus able to match the *a priori* interpretation of the 1986 length-frequency distribution reasonably well, using parameters from the secondary ridge crest (Fig. 8).

1987 distribution The first mode of this distribution is fairly pronounced and has been interpreted as age 1, but the modes following are not well defined (NSTC 1987; Fig. 2). SRLCA indicated best fitting parameter pairs in a primary score ridge ranging from L_{inf} = 35 mm, K = 0.50 to L_{inf} = 50 mm, K = 0.23, with a maximum at L_{inf} = 40 mm, K = 0.36, and in a secondary ridge ranging from L_{inf} = 32 mm, K = 0.50 to L_{inf} = 40 mm, K = 0.24, with a nonboundary local maximum at L_{inf} = 33 mm, K = 0.43 (Table 4, Fig. 9). The primary ridge parameters defined three age groups, correctly classifying the first mode, lumping shrimp between 19.0 and 25.0 mm as a second group, and aggregating all shrimp >25 mm as a final group. The secondary ridge parameters resolved the distribution in a similar manner, but by splitting shrimp >23 mm into two groups (Fig. 10). Thus, neither set of parameters selected by SRLCA successfully resolved shrimp between 19.0 and 25.0 mm to distinct cohorts.

1988 distribution In the 1988 survey length frequency, the large mode between 13 and 19 mm was assumed to be age-1 shrimp. A smaller mode of 20–23 mm was interpreted as age 2, with shrimp >25 mm assumed, as usual, to be age-group 4+ (NSTC 1988; Fig. 2). SRLCA provided two ridges of high scoring parameters, a primary ridge extended from a boundary max-

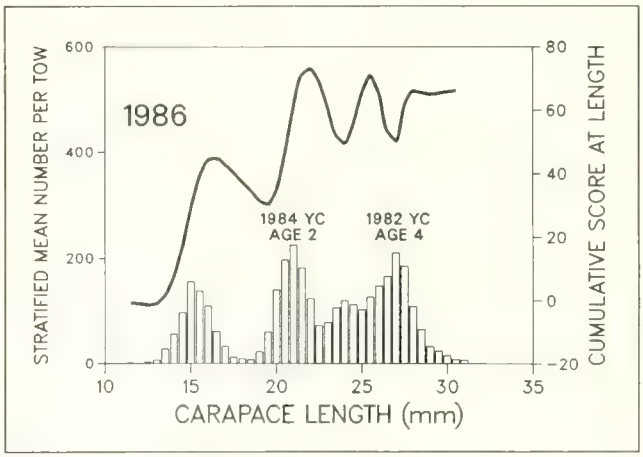

Figure 8

Northern shrimp survey 1986 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 33 mm, K = 0.42).

Table 4

Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1987 northern shrimp survey length-frequency distribution: primary and secondary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	35	0.50	55.0
	40	0.36	57.1[2]
	45	0.28	56.7
	50	0.23	55.9
Secondary ridge crest	32	0.50	42.5[1]
	34	0.39	40.1
	36	0.32	37.9
	38	0.28	35.5
	40	0.24	34.0
	33	0.43	41.3[3]

[1] High score parameters of ridge crest, on boundary of explored space.
[2] High score parameters of ridge crest, nonboundary maximum.
[3] Parameters selected for final evaluation.

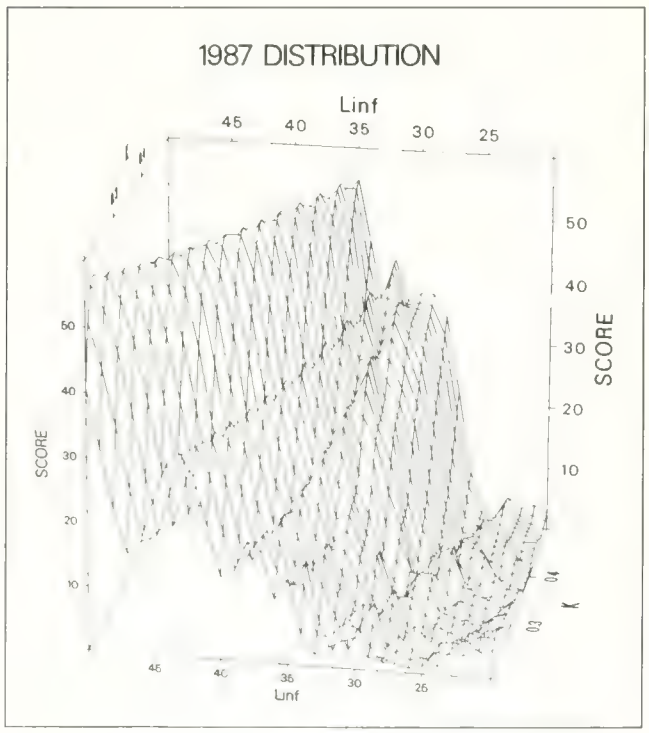

Figure 9

Response surface of the SRLCA score function for the northern shrimp survey 1987 length-frequency distribution.

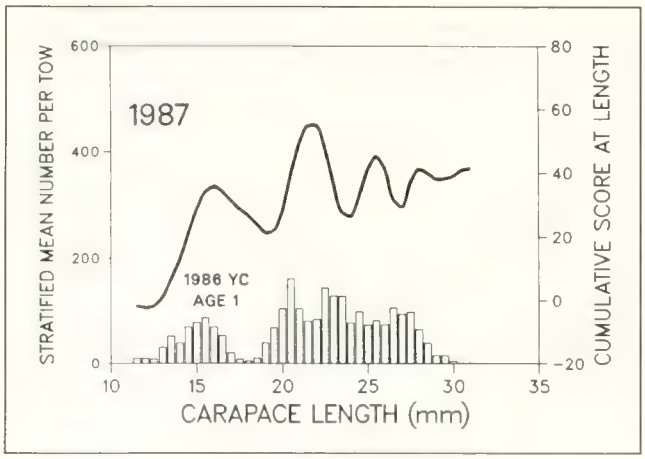

Figure 10

Northern shrimp survey 1987 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 33 mm, K = 0.43).

Table 5

Von Bertalanffy growth parameter pairs and SRLCA score (S) for 1988 northern shrimp survey length-frequency distribution: primary and secondary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	43	0.50	123.5[1]
	45	0.46	123.0
	47	0.42	122.4
	49	0.39	121.9
Secondary ridge crest	35	0.47	93.3[2,3]
	40	0.34	88.5
	45	0.25	85.0
	50	0.20	85.0

[1] High score parameters of ridge crest, on boundary of explored space.
[2] High score parameters of ridge crest, nonboundary maximum.
[3] Parameters selected for final evaluation.

imum at L_{inf} = 43 mm, K = 0.50 to L_{inf} = 49 mm, K = 0.39, while a secondary ridge ranged from L_{inf} = 35, K = 0.47 to L_{inf} = 50 mm, K = 0.20 (Table 5, Fig. 11).

Values from the primary ridge resolved shrimp 11–21.5 mm as a single cohort (age 1), with animals 22 mm and larger assigned to age 2. Values from the secondary ridge provided only a slightly improved interpretation, with shrimp 11–19.5 mm classified as age 1, 20–25 mm as age 2, and >25 mm as age 3. Clearly, the modes in this distribution were not sufficiently distinct to allow a reasonable interpretation using SRLCA (Fig. 12).

Pooled distribution: 1984–88 As with the annual distributions, an exploratory run was made with L_{inf} values ranging from 20–50 mm, in 1-mm steps, and K values of 0.20–0.50, in 0.01 steps. Two broad regions

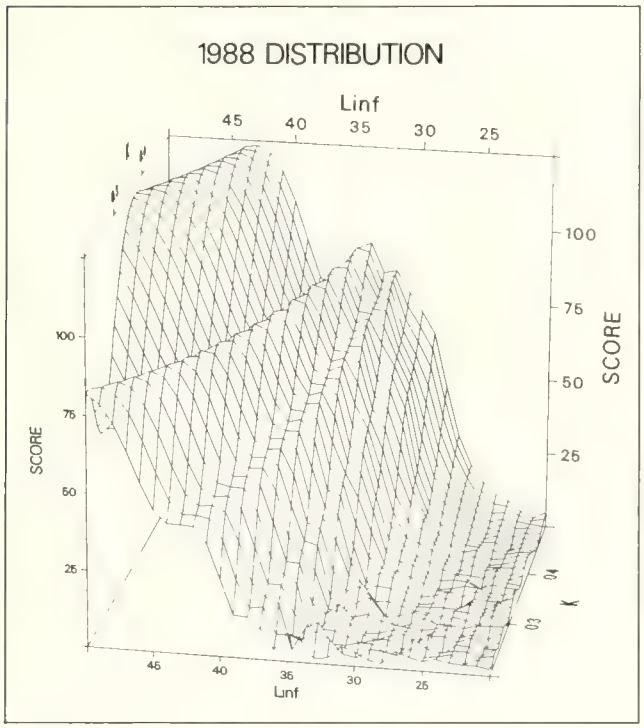

Figure 11
Response surface of the SRLCA score function for the northern shrimp survey 1988 length-frequency distribution.

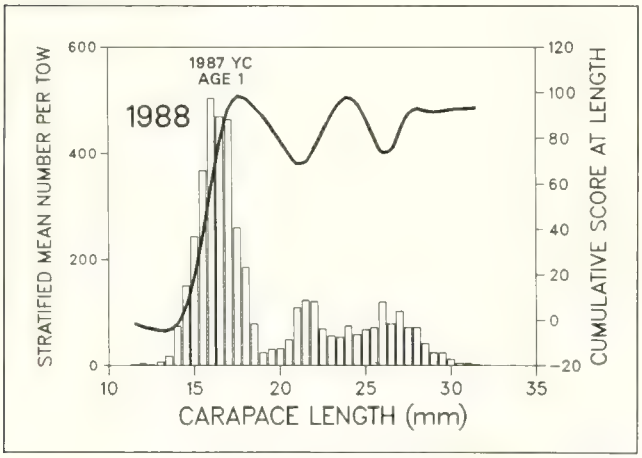

Figure 12
Northern shrimp survey 1988 length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 35 mm, K = 0.47).

of parameters, with a primary ridge in one region and secondary, tertiary, and quaternary ridges in the other, were evaluated in an attempt to find parameters selected by the SRLCA test function that would interpret the 1984–1988 distributions in accordance with *a priori* assumptions.

Table 6
Von Bertalanffy growth parameter pairs and SRLCA score (S) for pooled 1984–88 northern shrimp survey length-frequency distribution: primary, secondary, tertiary, and quaternary ridge crests.

	L_{inf} (mm)	K	S
Primary ridge crest	43	0.50	244.0
	44	0.47	244.8
	46	0.43	245.7
	48	0.40	246.5[2]
	50	0.37	247.8[1]
Secondary ridge crest	35	0.50	219.2
	35	0.48	227.0
	36	0.44	230.3
	38	0.38	233.7
	40	0.34	234.0
	42	0.30	234.9[2]
	44	0.27	234.2
	46	0.25	233.4
	48	0.23	232.5
	50	0.21	232.1
Tertiary ridge crest	32	0.50	190.0
	32	0.49	191.4[2]
	33	0.43	175.0
	34	0.39	160.0
	35	0.35	147.3
	37	0.29	127.9
	40	0.23	108.9
	43	0.20	98.3
Quaternary ridge crest	33	0.33	101.5
	33	0.32	104.6[2]*
	34	0.29	94.8
	35	0.26	88.2
	36	0.24	80.7
	37	0.22	76.2
	38	0.20	73.3

[1] High score parameters of ridge crest, on boundary of explored space.
[2] High score parameters of ridge crest, nonboundary maximum.
*Parameters selected for final evaluation.

The primary ridge ranged from L_{inf} = 43 mm, K = 0.50 to a boundary maximum at L_{inf} = 50 mm, K = 0.37. The highest nonboundary score was at L_{inf} = 48.0 mm, K = 0.40. A secondary ridge ranged from L_{inf} = 35 mm, K = 0.50 to L_{inf} = 50, K = 0.21, with a nonboundary maximum score at L_{inf} = 42.0, K = 0.30. A tertiary ridge ranged from L_{inf} = 32 mm, K = 0.50 to L_{inf} = 43 mm, K = 0.20, with a nonboundary maximum at L_{inf} = 32 mm, K = 0.49. A quaternary ridge ranged from L_{inf} = 33 mm, K = 0.33 to L_{inf} = 38 mm, K = 0.20, with a nonboundary maximum score at L_{inf} = 33 mm, K = 0.32 (Table 6, Fig. 13).

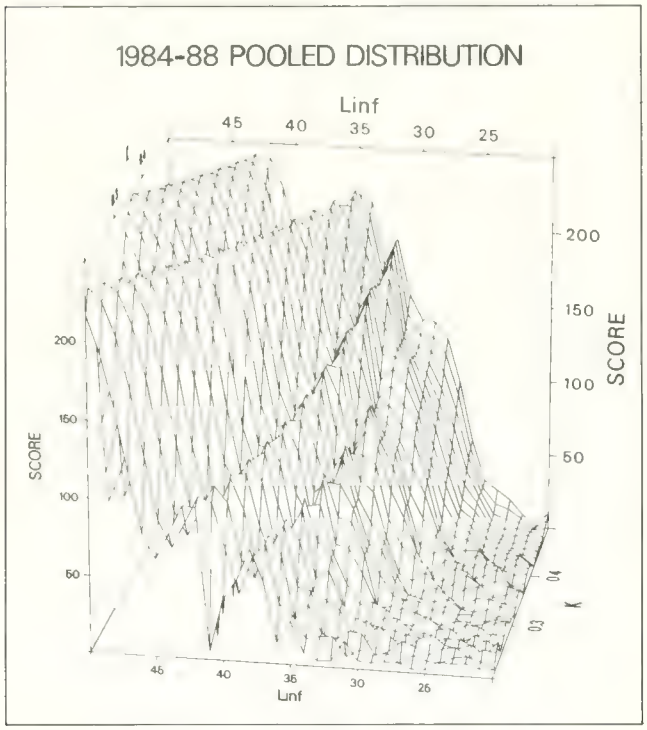

Figure 13

Response surface of the SRLCA score function for the northern shrimp survey 1984–88 length-frequency distribution.

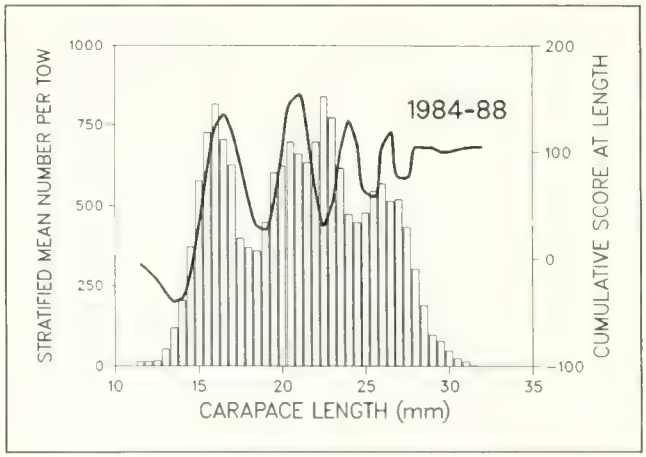

Figure 14

Northern shrimp survey 1984–88 pooled length-frequency distribution (histogram) and pattern of SRLCA scores (solid curve) for growth parameters selected for final evaluation (L_{inf} = 33 mm, K = 0.32).

Values from the primary ridge tended to treat the assumed first and second observed age-groups, up to 21 mm, as a single mode, with animals greater than 21.5 mm classified as age 2. Values from the secondary ridge accurately interpreted the assumed age-group 1, but lumped the assumed second and third age-groups as a single mode, with shrimp >25 mm classified as age 3. Values from the tertiary ridge also correctly characterized the first age group and failed to resolve the second and third modes to distinct age classes, but split shrimp >24 mm into age-groups 3 and 4. It is interesting to note that the two sets of previously derived von Bertalanffy parameters for this stock noted earlier (see Methods: *A Priori* Assumptions) fell within this tertiary ridge of scores. This indicated that growth rates based on those parameters were too fast to provide an interpretation of length distributions consistent with visual inspection of the length modes.

Quaternary ridge values successfully classified the first–fourth assumed age-groups in line with prior assumptions. These parameters also provided an age-group 5 for CL >27.5 mm. The quaternary ridge non-boundary maximum score parameters (L_{inf} = 33 mm, K = 0.32) were selected for final SRLCA evaluation of the pooled length frequency, as these values provided the characterization of the pooled distribution closest to the assumed age structure (Fig. 14). The growth curve defined by these parameters indicates a slower rate compared with previously estimated growth curves (data from Haynes and Wigley 1969, McInnes 1986), a result of the influence, or "bias," of the abundant, apparently slower-growing, 1982 cohort on the score function (Fig. 15).

We derived annual age frequencies by slicing annual length frequencies to age-groups according to the maximum-scoring growth parameters provided by the four score ridges of the pooled analysis (Table 6). Since shrimp of age-group 2 and older are assumed fully recruited to the survey trawl gear, total instantaneous mortality estimates (Z) were derived from:

$$Z = \ln\left(\sum \text{age } 2+ \text{ for Year}_N \,/\, \sum \text{age } 3+ \text{ for Year}_{N+1}\right).$$

These values were then compared with previously calculated estimates of total mortality from the length-frequency data (NSTC 1985, 1986, 1987, 1988).

Table 7 shows the widely divergent age frequencies and subsequent Z estimates provided by the four different pairs of growth parameters, which again illustrate a necessity for some external source of information to interpret SRLCA results in a manner consistent with a priori assumptions. We note that for the 1987 distribution, the quaternary ridge parameters and NSTC visual inspection sliced the length-frequency distribution at the same length intervals, resulting in identical age frequencies for 1987. As expected, use of the quaternary SRLCA score ridge parameters to

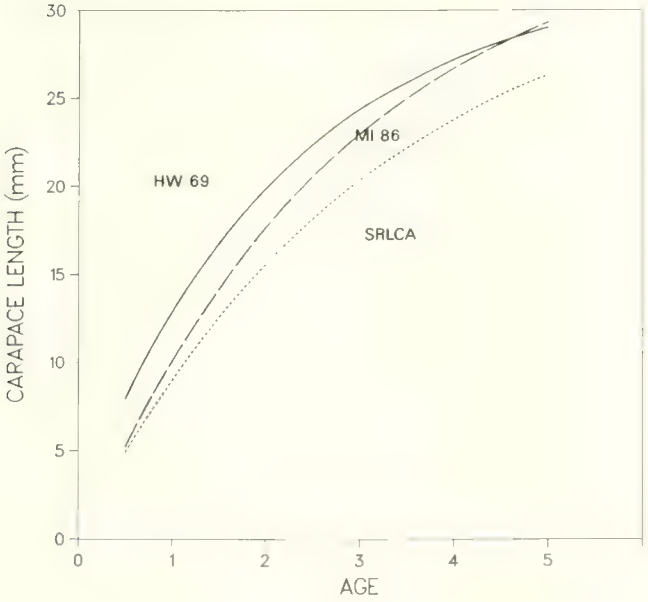

Figure 15

Von Bertalanffy growth curves for Gulf of Maine *Pandalus borealis*. Upper curve (solid line) is for parameters derived from age-length data in Haynes and Wigley (1969); center curve (large dashed line) is for growth parameters cited in McInnes (1986); lower curve (dot-dashed line) is for parameters derived by SRLCA for northern shrimp survey length-frequency data.

age the length frequencies provided mortality estimates consistent with those produced by visual inspection of length modes.

Discussion

We subjected SRLCA to a fairly stern test by attempting to interpret a data set exhibiting variable recruitment and growth patterns, and by using a broad initial parameter search space. As noted in the Monte Carlo tests of SRLCA by Basson et al. (1988), these variations in recruitment, and in mean length-at-age (presumed variable growth rate, especially for the abundant 1982 cohort) between cohorts, made interpretation of the northern shrimp length-frequency distributions difficult. The shape and proximity of the assumed age-2 and -3 modes frequently caused SRLCA to interpret these modes as a single age-group, resulting in highest scoring parameters that provided positively biased estimates of growth rate. This problem was most severe for the annual distributions and persisted in the pooled length frequency, although the increased amount of information in the pooled distribution did increase the effectiveness of the SRLCA approach, with a "correct" interpretation of the data available from the quaternary score ridge. Analysis of the pooled data in a truly sequential fashion, after the projection matrix approach of Rosenberg et al. (1986) and Basson et al. (1988), as a supplement to SRLCA might help in alleviating these problems.

This exercise demonstrated that the best objective fit obtained by SRLCA does not necessarily provide the best interpretation of the data, as with most of the existing length-frequency distribution analysis methods. Pragmatically, we could not rely on SRLCA to provide a single set (or even region) of growth parameters that yield both the highest parameter score and the "correct" interpretation of the data, unless supple-

Table 7

Age-frequency matrices and instantaneous total mortality rates (Z) for age 2+ northern shrimp estimated by growth parameters from SRLCA high-score parameter ridges for the 1984–88 pooled distribution, compared with estimates using method of visual inspection of length modes (NSTC 1984, 1985, 1986, 1987, 1988).

Age	1984	1985	1986	1987	1988
SRLCA					
Primary score ridge					
1	2150	887	1489	1091	3192
2	856	2644	1872	1357	1136
3	0	0	0	0	0
4+	0	0	0	0	0
	Z_{84} = ···	Z_{85} = ···	Z_{86} = ···	Z_{87} =	
Secondary score ridge					
1	633	660	753	575	2903
2	2001	2083	1504	1257	818
3	373	789	1104	620	604
4+	0	0	0	0	0
	Z_{84} = 1.10	Z_{85} = 0.96	Z_{86} = 1.44	Z_{88} = 1.13	
Tertiary score ridge					
1	672	660	755	577	2906
2	1853	1849	1283	1088	693
3	410	876	857	545	504
4+	71	146	465	239	224
	Z_{84} = 0.83	Z_{85} = 0.78	Z_{86} = 1.20	Z_{88} = 0.94	
Quaternary score ridge					
1	193	634	701	539	2564
2	1987	350	845	575	632
3	425	1710	615	663	433
4+	401	837	1200	671	699
	Z_{84} = 0.10	Z_{85} = 0.47	Z_{86} = 0.69	Z_{88} = 0.52	
NSTC					
Visual inspection					
1	49	646	710	539	2828
2	2051	337	959	575	614
3	442	1596	491	663	187
4+	463	952	1200	671	699
	Z_{84} = 0.15	Z_{85} = 0.53	Z_{86} = 0.69	Z_{88} = 0.77	

mented by an external source of information. For SRLCA to be effective, the subjectivity required in the selection of input parameters for use with the family of distribution mixture methods (e.g., MacDonald and Pitcher 1979) must instead be applied to interpretation of the output of the procedure.

These problems are similar to those encountered by others in evaluating the ELEFAN I method of Pauly and David (1981). Testing of ELEFAN I has indicated it produces biased results unless the range of growth parameters considered for testing is relatively narrow, and that it is sensitive to increased variation in length-at-age or increased variation in recruitment timing (Rosenberg and Beddington 1987). Recent work by Morgan (1987), supplementing ELEFAN with age-length data, improved the performance of that method by allowing selection of the appropriate parameters from among several locally optimal solutions.

We are encouraged, however, that such external information requirements were moderate for SRLCA. For instance, with an expectation of age of the oldest cohort, we would have immediately selected the quaternary ridge of the pooled analysis as best. Or, had we limited the initial search space for L_{inf} to within 10% of the CL of the largest animal, and/or 10% of an "average" L_{inf} given previously derived parameters (e.g., 33 ± 2 mm), we again could have proceeded directly to selection of the appropriate score ridge.

Even given conditions of variable growth and recruitment, we were able to inspect the response surface of the test function and, using a moderate degree of subjectivity and a stepwise procedure of evaluation, select growth parameters from alternative high-score ridges that resolved the pooled distribution in a manner consistent with previous interpretations, and, more important, in a more satisfactory manner than previously derived von Bertalanffy growth parameters. Overall we found SRLCA to be a simple and generally effective tool for the estimation of growth parameters, and subsequently age frequencies, from length-frequency distributions for Gulf of Maine northern shrimp.

Acknowledgments

We thank the ships officers, crew, and scientific staff of the RV *Gloria Michelle* and the members of the Northern Shrimp Technical Committee for their efforts in collecting the data on which this paper is based. We also acknowledge Dr. Steve Clark, Dr. Wendy Gabriel, the members of the 1989 NAFO Working Group on Progress in Age Determination of *Pandalus*, and an anonymous reviewer for their valuable comments on the manuscript.

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Abstract.—Gonad-somatic index (GSI), the relation of ovarian to somatic weight, was calculated for 14 species of finfish that are yearlong residents of the New York Bight. Specimens were collected monthly from June 1974 through June 1975 in the ocean and associated estuarine waters of the Bight. Analysis indicated that alewife and yellowtail flounder are spring spawners; silver and red hake, black sea bass, butterfish, striped and northern searobin, and fourspot flounder are summer spawners; and summer and winter flounder are fall-winter spawners. Offshore hake exhibited a protracted spawning season with ripe females collected from spring through fall, while spotted hake and windowpane exhibited bimodal spawning patterns with two GSI peaks per year. The co-occurrence of spawning with appropriate food supply and environmental conditions is discussed on an individual-species as well as species-complex basis.

Annual Cycles of Gonad-Somatic Indices as Indicators of Spawning Activity for Selected Species of Finfish Collected from the New York Bight

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In temperate zones, reproduction of marine fish species is usually characterized by single annual peaks of spawning activity (Cushing 1969). Seasonal changes in the gonads of fishes, in preparation for reproduction, are known to be controlled by hormones, and triggered, sometimes well in advance of spawning, by photoperiod (Hoar 1969, Bye 1984). Minor variations in spawning time, during any given year, are believed to be related to temperature and to the overall condition of the fish (de Vlaming 1972, Bye 1984). Wootton (1984) defines reproductive "strategies" as the genetically determined pattern of spawning behavior, and reproductive "tactics" as the responses to exogenous cues during a single season.

The gonad-somatic index (GSI), the relation of ovarian weight to somatic weight, provides a measure of spawning readiness while removing variability attributable to fish size (Nikolskii 1963). The GSI has also been termed the gonosomatic index (de Vlaming et al. 1982) and maturity index (Morse 1981). Annual cycles in GSI can be thought of as an approximate measure of the energy expended for reproduction, which makes this information critical in formulating energy budgets relating to the balance between fish production and consumption.

Approximate spawning times for the most common species which occur in the New York Bight have been established based on the distribution of eggs and larvae (Colton et al. 1979) and published life-history information (Grosslein and Azarovitz 1982). However, detailed qualitative and quantitative information on annual cycles of spawning as determined by examination of maturity stages is lacking for many, if not most, of these same species. This study presents monthly variations in GSI as they relate to hydrographic observations for 14 species of fish which represent many of the dominant fishes found on the Middle Atlantic continental shelf and in associated estuarine waters (Wilk and Silverman 1976ab, Wilk et al. 1977; Colvocoresses and Musick 1984).

Materials and methods

Fish were collected from June 1974 to June 1975 during monthly bottom surveys in the central portion of the New York Bight at the confluence of the Long Island, New York and New Jersey coastlines and the contiguous Sandy Hook-Lower-Raritan Bay estuary (Fig. 1). This area is characterized by seasonally intensive recreational and commercial fisheries and is influenced by a wide variety of anthropogenic activities (Gross 1976, Mayer 1982).

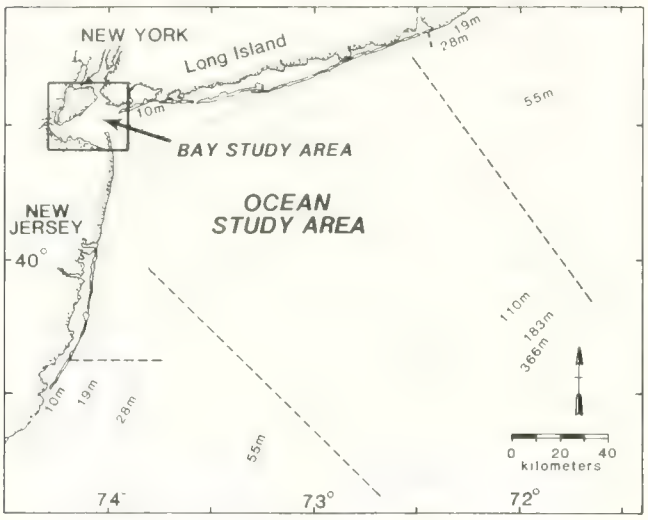

Figure 1

Middle Atlantic continental shelf with outlines of the ocean and estuarine (bay) study areas where finfish were sampled during a trawl survey of the New York Bight, June 1974–June 1975.

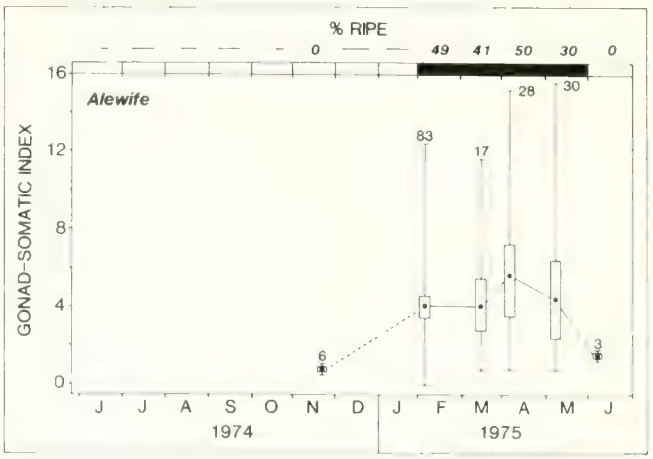

Figure 2

Annual cycle of gonad-somatic indices for alewife *Alosa pseudoharengus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

Two study areas, ocean and estuarine, were designated (Fig. 1). The ocean area was delineated by an imaginary set of lines extending seaward from points on Long Island, New York and New Jersey to the 28-m isobath and from the 28-m isobath to the edge of the continental shelf (366 m). This area corresponds to offshore strata 1–4 and inshore strata 6–17 of the Northeast Fisheries Center's resource trawl survey (Grosslein 1969). The estuarine study area included Sandy Hook, Lower, and Raritan bays.

Station locations in the ocean study area were selected by stratified random sampling design (Grosslein 1969). Strata boundaries were determined by depth as follows: 0–10, 11–19, 20–28, 29–55, 56–110, 111–183, and 184–366 m. A minimum of two stations per stratum was selected randomly to be sampled during each cruise. Inshore (0–28 m) and offshore (29–366 m) strata were sampled at rates of approximately one station per 515 and 1030 km^2, respectively. An average of 49 ocean stations was sampled per cruise. Ocean stations were not sampled during December 1974 and January 1975.

The estuarine study area was divided into 103 potential sampling blocks. Except where interrupted by land, each block measured 1′ of latitude by 1′ of longitude, i.e., 1.8 km × 1.4 km (2.5 km^2). A set of stations was selected randomly from these blocks and retained throughout the study. An average of 15 estuarine stations was sampled per cruise. Estuarine stations were not sampled during December 1974.

Fish collections were made with otter trawls towed at approximately 6.5 km/hour for 15 and 30 minutes at estuarine and ocean stations, respectively. Estuarine stations were sampled with a 9.1-m trawl and ocean stations with a Yankee #36 trawl. All specimens of each species, up to 35 individuals from each trawl station, were selected and frozen for later laboratory analysis. If the total catch of a species exceeded 35 individuals, a size-stratified sample of 25 to 35 specimens was frozen. At the laboratory each specimen was measured from the snout to the extent of the middle caudal fin ray (±1.0 mm), weighed (±0.1 g), sexed, and state of maturity determined by macroscopic evaluation when possible. Stage of ovarian development was determined visually, and designated immature, developing, ripe, or resting. Ovaries were weighed (±0.01 g) and GSI calculated (ovarian weight/fish weight × 100). It should be noted that only mature females were included in the calculation of GSI.

Temperature and depth observations were made at all stations. Vertical temperature profiles were obtained with expendable bathythermographs during ocean cruises and with portable temperature probes during estuarine cruises. Fathometers continually recorded depth during each trawl tow. Detailed information relative to survey design, methodology, species distribution and abundance, and associated hydrographic observations is given in Wilk et al. (1977).

Results

The majority (93%) of all ripe females collected during the survey were caught in the ocean study area. Of the

Table 1

Observations relative to peak spawning activity for 14 finfish species, including mean and range of bottom temperature and depth for the month, or months, of highest gonad-somatic indices (GSI) at stations where ripe females occurred during a trawl survey of the New York Bight, June 1974–June 1975. Alewife and winter flounder data include only estuarine observations; bimodal spawners are indicated with an asterisk (*) with observations given for both peaks; in some cases months were combined when sample sizes were small.

Species	Month	No. of fish	Occurrence/total no. of stations	Bottom temperature (°C)		Depth (m)	
				Mean	Range	Mean	Range
Alewife	Apr 75	18	7/14	5.4	4.5–6.0	6	5–11
Offshore hake	May/Jun 75	17	4/156	10.2	9.0–11.4	270	222–348
Silver hake	Aug 74	5	4/58	9.8	8.4–13.4	80	54–127
Red hake	Jun 75	68	23/72	8.0	5.7–12.5	60	12–264
Spotted hake*	Sep 74	42	7/56	14.8	11.0–17.3	30	12–86
Spotted hake*	Mar/Apr 75	10	4/109	10.5	7.4–12.3	113	75–139
Black sea bass	Jul 74	16	3/59	14.9	13.8–15.9	19	16–22
Butterfish	Jun 74 & 75	189	45/130	11.8	5.4–20.4	40	3–145
Northern searobin	Jul 74	21	8/59	15.1	13.8–16.5	20	15–27
Striped searobin	Jun 74 & 75	12	8/130	10.9	8.4–14.1	16	9–21
Summer flounder	Oct 74	51	22/60	13.7	10.5–14.7	35	11–97
Fourspot flounder	Jun 75	32	15/72	7.3	5.6–11.2	57	17–127
Windowpane*	Sep 74	150	23/56	15.7	10.3–19.4	26	10–65
Windowpane*	May 75	159	44/84	7.9	5.6–13.2	23	4–51
Yellowtail flounder	Mar 75	45	15/46	5.7	4.4–7.5	36	9–68
Winter flounder	Jan 75	5	3/9	5.7	4.8–6.5	5	3–7

total catch of ripe female alewife and winter flounder, 5 and 21%, respectively, were collected in the estuarine study area. This was expected since these species are known to inhabit the lower reaches of estuaries before moving upriver to spawn. Ripe female butterfish and windowpane were also collected in the estuarine study area, but made up <5% of the catch of all ripe females of those species. Eggs and larvae of these four species are known to occur in both Raritan Bay (Croker 1965) and the New York Bight (Clark et al. 1969; Smith et al. 1975, 1980). Silver hake, red hake, and summer flounder were also caught in the estuarine study area during some months; however, no ovarian development beyond the resting stage was observed. All data were pooled since there were no clear differences in time of spawning between bay and ocean samples of any species captured during the study. Detailed results and discussion for each species are given in the following sections.

Alewife *Alosa pseudoharengus*

Mean GSI was highest in April, with ripe females, 145–345 mm, collected throughout the survey area from February through May (Fig. 2). These observations are similar to published spawning times for alewife in Connecticut inshore waters (Kissil 1969) and the Delaware River (Smith 1971). Farther north in Canadian waters the species spawns primarily in May (Leim and Scott 1966).

Alewives are common in coastal waters from Newfoundland, Canada to North Carolina as they migrate to and from their riverine spawning grounds (Hildebrand and Schroeder 1928, Bigelow and Schroeder 1953, Leim and Scott 1966). The average temperature in the estuarine survey area during the April spawning peak was 5.4°C (Table 1).

Offshore hake *Merluccius albidus*

Mean GSI was highest during July 1974 and again in June 1975, with ripe females, 230–575 mm, collected in ocean waters during most months sampled (Fig. 3). The highest percentages of ripe ovaries were observed in spring and summer. In a review of historic ichthyoplankton surveys, Colton et al. (1979) stated that offshore hake larvae were present in the Middle Atlantic from June through September. Smith et al. (1980) collected eggs and larvae south of New England from April through June during 1977–79 ichthyoplankton surveys. They also collected eggs in late February–early March 1979 from stations south of Long Island, New York. Marak (1967) found eggs and larvae off Martha's Vineyard, Massachusetts, in April through July. Offshore hake, based on this as well as the aforementioned studies, has either a long or irregular spawn-

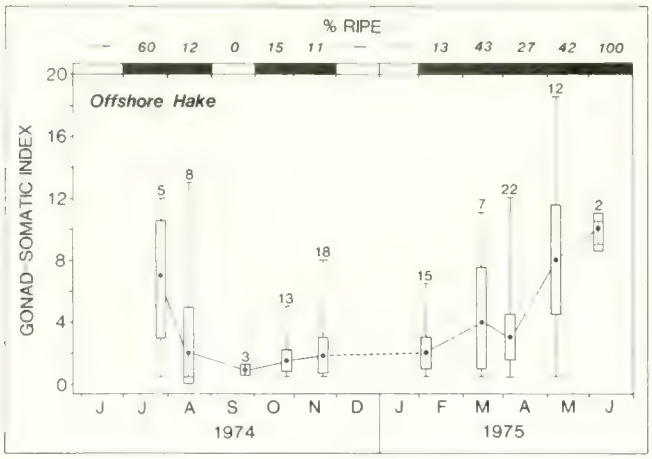

Figure 3

Annual cycle of gonad-somatic indices for offshore hake *Merluccius albidus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

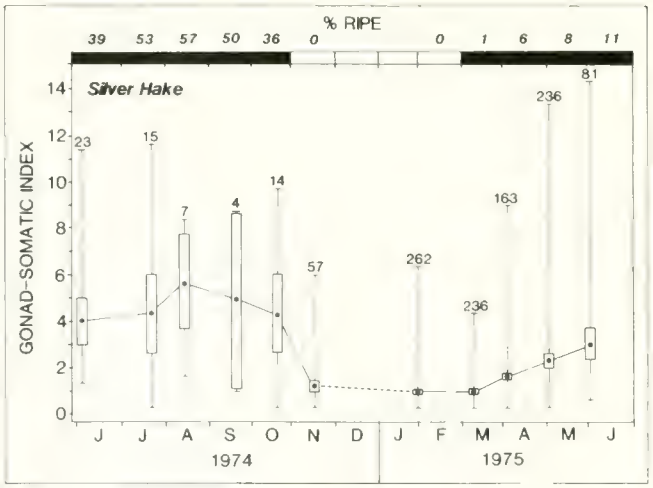

Figure 4

Annual cycle of gonad-somatic indices for silver hake *Merluccius bilinearis* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

ing season or perhaps even spawns continually throughout the year.

Offshore hake range from Georges Bank to the coast of South America along the continental shelf break in depths >100 m (Bigelow and Schroeder 1955, Leim and Scott 1966). They are the deepest ranging species described in this study, being found between 162 and 366 m, the survey extreme. They were collected within a relatively restricted temperature range throughout the year, with little or no seasonal changes.

Silver hake *Merluccius bilinearis*

Ripe females, 202–590 mm, were collected in ocean waters during a long spawning season, March through October, with mean GSI highest from July to October (Fig. 4). A protracted spawning season for this species in the Middle Atlantic is supported by two ichthyoplankton surveys: (1) Fahay (1974) collected eggs during 1966 from May through November with a peak in June–July; and (2) Sherman et al. (1984) reported larvae were collected during 1977–79 from April through November, with a peak in August.

Silver hake are found over all bottom types from the intertidal zone to the 200-m isobath from Nova Scotia, Canada to Cape Hatteras, North Carolina (Bigelow and Schroeder 1953, Leim and Scott 1966). During August, the month of highest mean GSI, silver hake were found well offshore where temperatures were moderate (Table 1). During the remainder of the year females were captured throughout the entire survey area at a wide variety of depths (4–335 m) and temperatures (4.3–19.2°C).

Red hake *Urophycis chuss*

Mean GSI was highest during the summer; however, ripe females, 225–621 mm, were present from May through September (Fig. 5). Colton et al. (1979) reported the occurrence of larvae in the Middle Atlantic from May through October with a peak in June or July. Off the southern New England coast, adults migrate offshore to the continental slope and spawn during May through September at temperatures of 5–11°C (Musick 1969, 1974).

Red hake were among the deepest spawners observed during the study with a mean capture depth of 60 m in June 1975 during the height of the spawning cycle (Table 1). The mean temperature of 8.0°C at time of spawning agrees with previously reported observations. It is noteworthy that five specimens in spawning condition were caught at two nearshore ocean stations at which the depth and temperature were 25 and 27 m and 15.3 and 17.1°C, respectively. These observations, to some degree, broaden the spawning depth and temperature ranges reported by Musick (1969, 1974).

Spotted hake *Urophycis regia*

Spotted hake exhibited a bimodal or split spawning pattern which was characterized by two mean GSI peaks,

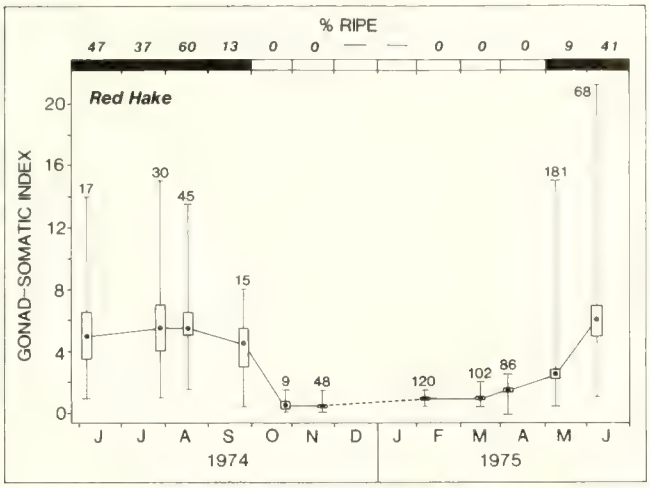

Figure 5

Annual cycle of gonad-somatic indices for red hake *Urophycis chuss* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

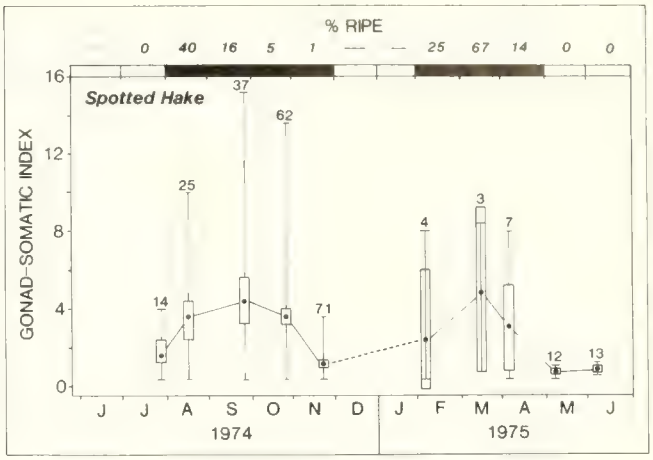

Figure 6

Annual cycle of gonad-somatic indices for spotted hake *Urophycis regia* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

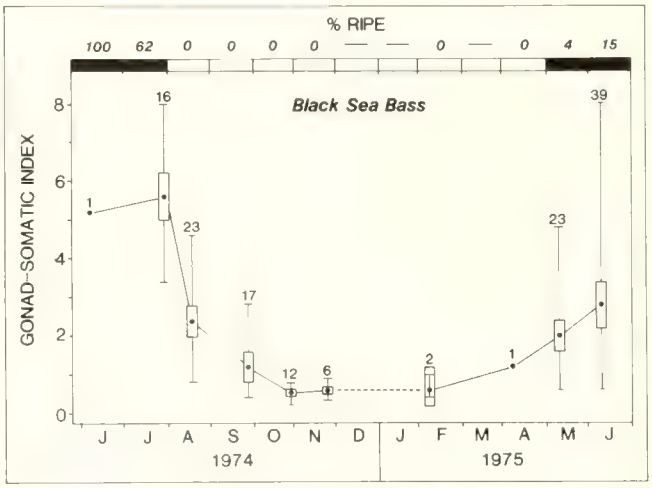

Figure 7

Annual cycle of gonad-somatic indices for black sea bass *Centropristis striata* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

one during March followed by another in September (Fig. 6). Ripe females, 283–396 mm, were collected from February through April. In addition, ripe females, 191–360 mm, were present again from August through November. Colton et al. (1979) suggested a spawning time of August through April with an October peak, but did not allude to a bimodal spawning pattern. Barans (1969) observed ripe females, with a minimum length of 225 mm, in the Chesapeake Bight from August through November. In collections made off the Carolinas, ripe spotted hake were found during December (Bigelow and Schroeder 1953).

In the September sample, ripe females were caught at depths between 12 and 86 m and temperatures of between 11.0 and 17.3°C. In contrast, during March and April ripe females were caught at much deeper and cooler locations (Table 1). Spotted hake range from southern New England to Florida (Hildebrand and Schroeder 1928, Bigelow and Schroeder 1953); however, they are most abundant south of Chesapeake Bay (Barans 1969). In the Chesapeake Bight, Barans (1969) reported their temperature range as 6–20°C, with a preferred range of 10–12°C. In addition, he gave 190 mm as the minimum length for 1-year-old females, and >280 mm for 2-year-olds. If the spotted hake captured during this study follow the size at ages given by Barans (1969), the population present in spring is composed primarily of older fish, with young-of-the-year and yearlings migrating into the area during summer and fall. The apparent split spawning season observed during this study may be attributable to dissimilar distributional patterns of specific age groups at the northernmost extreme of the species range.

Black sea bass *Centropristis striata*

Mean GSI was highest during July, with ripe females, 184–452 mm, collected from May through July (Fig. 7). Black sea bass are protogynous hermaphrodites with the size at which females become males extremely

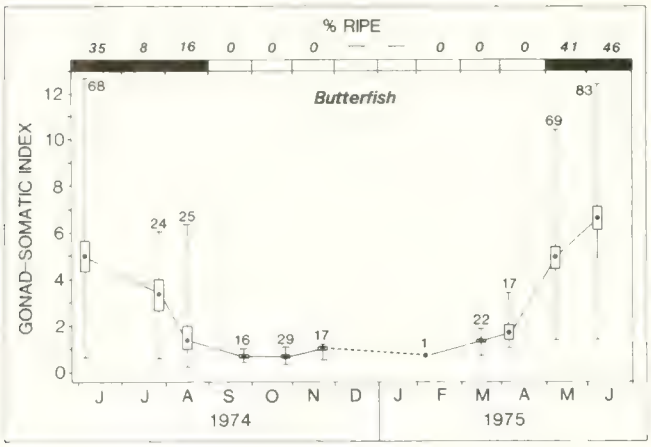

Figure 8

Annual cycle of gonad-somatic indices for butterfish *Peprilus triacanthus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

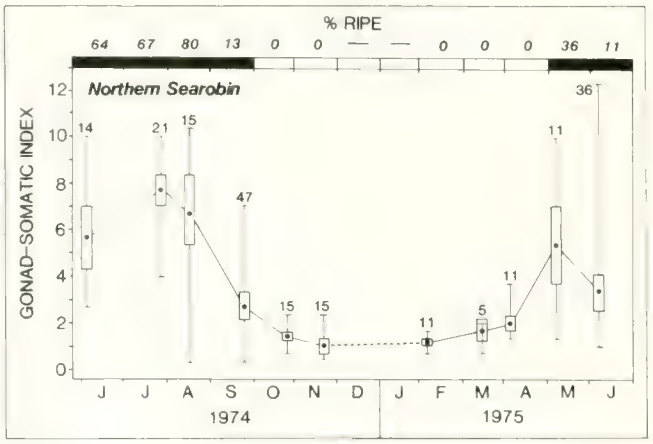

Figure 9

Annual cycle of gonad-somatic indices for northern searobin *Prionotus carolinus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

variable (Kendall and Mercer 1982). In this study female and male black sea bass were in the range 173–452 and 178–556 mm, respectively. Bigelow and Schroeder (1953) reported spawning from mid-May through June off southern New England and New Jersey. To date, black sea bass eggs have not been reported from plankton collections. However, larvae have been collected from Long Island, New York waters from mid-May to June (Perlmutter 1939) and from offshore New York Bight waters from June through November (Kendall 1977).

Black sea bass are common from Cape Cod, Massachusetts to Florida (Hildebrand and Schroeder 1928, Bigelow and Schroeder 1953). In the Middle Atlantic, they migrate northward and inshore in spring and offshore and southward in fall (Kendall and Mercer 1982). Mean temperature and depth of occurrence in July, the month of highest mean GSI, were among the warmest and shallowest of the survey (Table 1).

Butterfish *Peprilus triacanthus*

Highest mean GSI occurred in June 1974 and again in May and June 1975, with ripe females, 124–242 mm, being present throughout the survey area from May through August (Fig. 8). The butterfish is a migratory semi-pelagic species which ranges from Newfoundland, Canada to Florida (Bigelow and Schroeder 1953, Leim and Scott 1966). Colton et al. (1979) reported butterfish spawning in the Middle Atlantic from May through October with a peak in July or August. Smith et al. (1980) collected eggs off North Carolina during spring and larvae off New Jersey during early summer. Kawahara (1978) reported the spawning time of butterfish in the Middle Atlantic as April or May through August. Butterfish were collected at a wide range of temperatures and depths during the months of peak GSI (Table 1).

Northern searobin *Prionotus carolinus*

Highest mean GSI was in July; however, ripe females, 143–341 mm, occurred from May through September (Fig. 9). According to Richards et al. (1979), based on data from the north shore of Long Island, New York, GSI rose early in May, peaked in late May, and declined gradually through June and July. Colton et al. (1979) reported spawning from Block Island, Rhode Island to Cape Hatteras, North Carolina from May through November.

Eggs and larvae of *Prionotus* spp. are among the dominant ichthyoplankton occurring in the Middle Atlantic from New Jersey to Cape Hatteras, North Carolina during June through October (Smith et al. 1980, Sherman et al. 1984). This survey demonstrated that northern searobin favored warm shallow inshore waters during peak spawning (Table 1); however, from November through April they favored depths >50 m.

Striped searobin *Prionotus evolans*

Highest mean GSI occurred during June and July 1974 and again in June 1975, with ripe females, 204–414 mm, present from May through August (Fig. 10). Richards et al. (1979) determined spawning time for striped searobin to be almost the same as northern

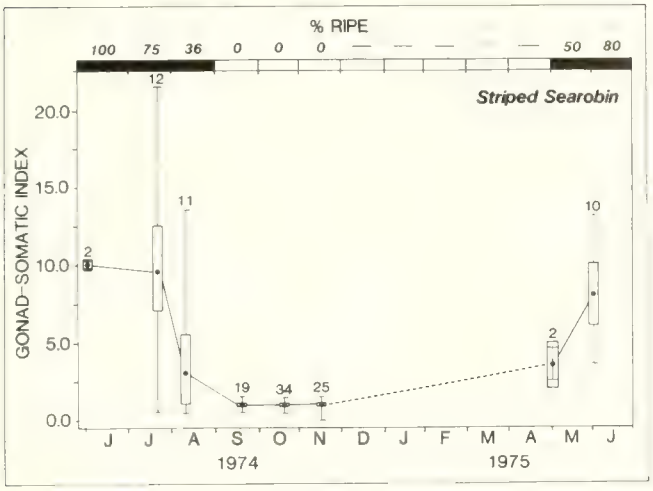

Figure 10

Annual cycle of gonad-somatic indices for striped searobin *Prionotus evolans* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

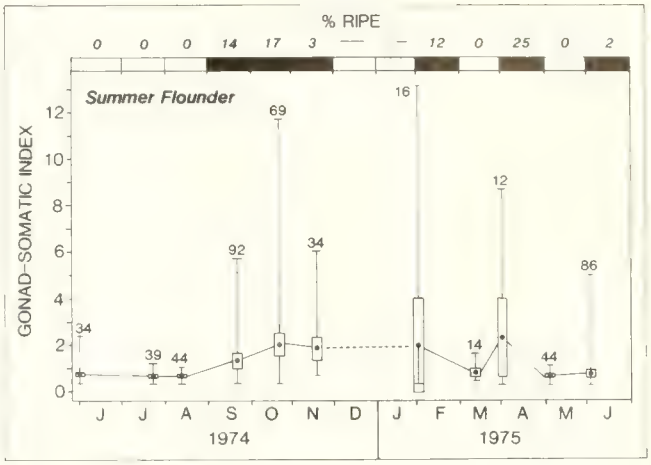

Figure 11

Annual cycle of gonad-somatic indices for summer flounder *Paralichthys dentatus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

searobin. Perlmutter (1939) collected larvae off Long Island, New York between May and June; and Herman (1963) reported spawning from June through August off Narragansett Bay, Rhode Island.

This study indicated temperature preferences during spawning were somewhat cooler than those of the northern searobin, while depths were similar (Table 1). However, throughout the remainder of the year, striped searobin were collected in comparatively warmer and shallower waters than northern searobin.

Summer flounder *Paralichthys dentatus*

Ripe females, 309–716 mm, were collected from September through November, and sporadically from February to June (Fig. 11). Although there were several slight peaks in GSI during the spawning season, these probably resulted more from individual sample variability than actual peaks in spawning activity (Fig. 11). Morse (1981), using additional maturity data from the New York Bight, reported spawning from September through March with a peak in October. Smith (1973) reported that eggs and larvae began to appear in September off Long Island, New York and southern New England, and occurred farther southward as fall progressed. After December, recently hatched larvae were common only south of Chesapeake Bay (Smith 1973).

Summer flounder range between Nova Scotia, Canada and Florida with their center of abundance lying in the Middle Atlantic region (Leim and Scott 1966, Gutherz 1967, Wilk et al. 1980). They migrate to shallow coastal waters and bays in summer, then offshore in fall (Bigelow and Schroeder 1953). At the GSI peak in October, developing females were collected in relatively warm shelf waters (Table 1). Depths of collection for summer flounder varied during the year, from a mean of 11 m in July to 92 m in April, reflecting their seasonal migration pattern.

Fourspot flounder *Paralichthys oblongus*

Mean GSI were highest in June and July 1974 and again in June 1975, with ripe females, 153–419 mm, present from April through September (Fig. 12). Smith et al. (1975) found small larvae off North Carolina and Chesapeake Bay in May and June, and off New Jersey and New York in July and August.

Fourspot flounder are widely distributed on the continental shelf between Georges Bank and Cape Hatteras, North Carolina (Bigelow and Schroeder 1953, Gutherz 1967). In the New York Bight, they inhabit the entire shelf, with deepest occurrences during winter (Ralph 1982). Collections from this survey indicate they were deepest during February and March, averaging 90 and 92 m, respectively, moving somewhat inshore during the rest of the year, but always at depths averaging >40 m. They were collected over a wide range of depths and temperatures during the June spawning peak (Table 1). Smith et al. (1975) collected larvae between 6 and 9°C at depths of 35–80 m.

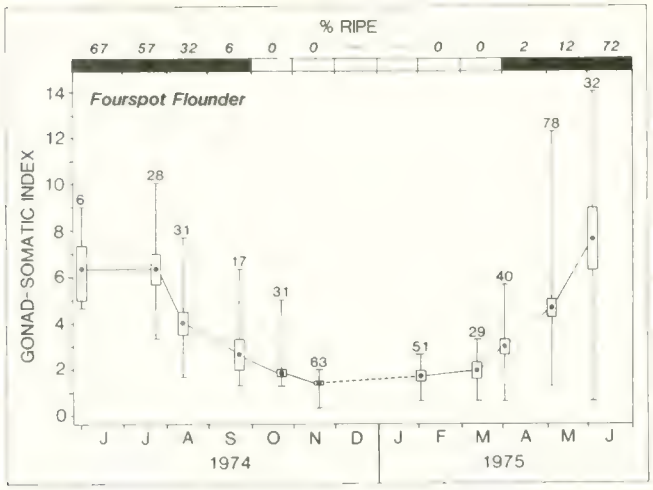

Figure 12

Annual cycle of gonad-somatic indices for fourspot flounder *Paralichthys oblongus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

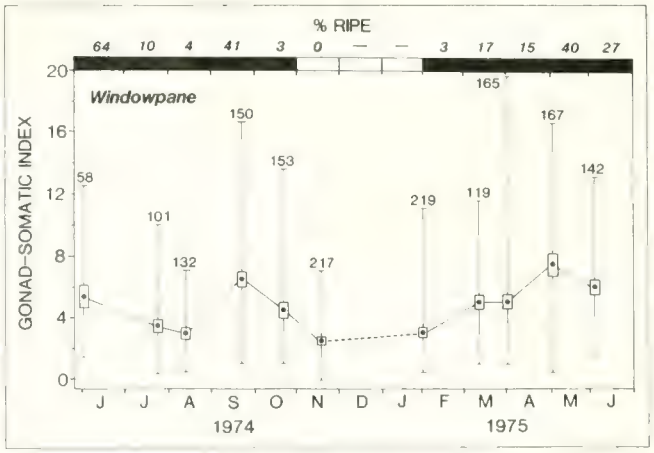

Figure 13

Annual cycle of gonad-somatic indices for windowpane *Scophthalmus aquosus*, collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

Windowpane *Scophthalmus aquosus*

The GSI plot for windowpane was bimodal, with peaks in May and again in September (Fig. 13). Ripe females, 201–387 mm, were collected from February through October, indicating that windowpane may spawn to some degree in the New York Bight during most of the year. Unfortunately, data for winter are lacking. There was no conclusive evidence that the two peaks represented spawning of either different populations or age classes. In September the mean lengths were 261 and 230 mm for females and males, respectively; in May, windowpane were somewhat more abundant and larger with mean lengths of 285 and 247 mm for females and males, respectively.

Split spawning of windowpane has been reported previously in the Middle Atlantic region. In 1952 and 1953, Wheatland (1956) found eggs from May through early July and again from late September through November in Long Island Sound, New York. Temperatures in the Sound were >20°C from late July through September when eggs were not present. Smith et al. (1975) proposed two patterns of spawning for windowpane depending on latitude. First, off New Jersey and New York one prolonged spawning season was hypothesized based on the occurrence of 2–6 mm larvae on the inner shelf from June through December 1966. Bottom temperatures on the inner shelf that year ranged between 6 and 17°C during August (Clark et al. 1969). Second, off Virginia and North Carolina spawning was interrupted as indicated by the occurrence of larvae in April through June and again in November and December 1966. During summer 1966 bottom temperatures ranged between 15 and 25°C (Clark et al. 1969). Smith et al. (1975) therefore concluded that in waters >20°C windowpane stop spawning.

Windowpane were collected during the May GSI peak at 5.6–13.2°C and 4–51 m; while during the September peak they were collected at higher temperatures but at similar depths (Table 1). In July and August, when GSI decreased noticeably, maximum bottom temperatures were 20–22°C at nearshore stations. Based on the results of this survey, coupled with the previously cited historical observations, a split spawning season is probably typical for windowpane in the New York Bight with continuous spawning occurring only during unusually cold summers.

Yellowtail flounder *Limanda ferruginea*

Highest mean GSI occurred from February to April, with ripe females, 212–422 mm, collected in October and November and February through May (Fig. 14). Howell (1983) observed female yellowtail off Rhode Island beginning to mature in September, with the peak GSI in April. Colton et al. (1979) reported spawning in the Middle Atlantic from April through August with peaks in May and June. Smith et al. (1975) found the largest concentrations of larvae off New Jersey in April and May. They also reported larvae in abundance off southern New England in May and June.

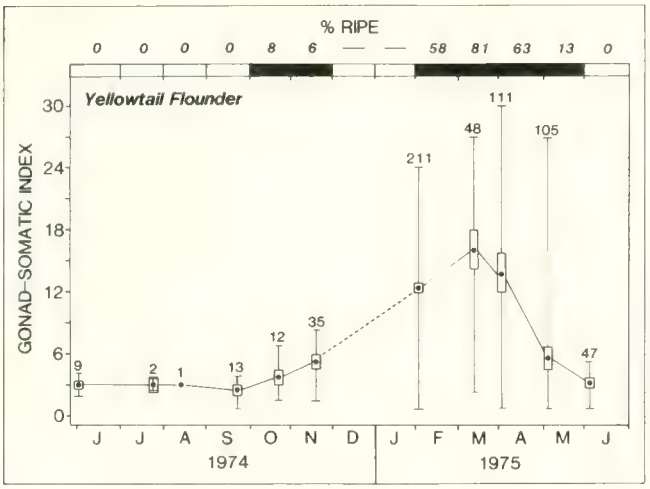

Figure 14

Annual cycle of gonad-somatic indices for yellowtail flounder *Limanda ferruginea* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

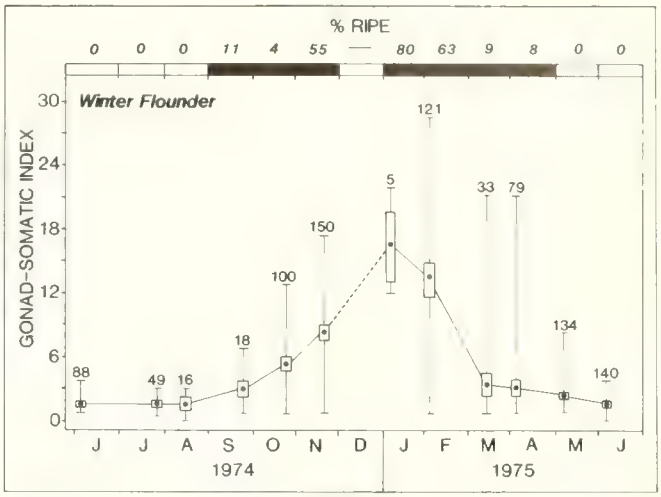

Figure 15

Annual cycle of gonad-somatic indices for winter flounder *Pseudopleuronectes americanus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

Yellowtail flounder commonly occur from Nova Scotia, Canada to Delaware Bay (Bigelow and Schroeder 1953, Leim and Scott 1966). Smith et al. (1975) considered the population center to be on Georges Bank, with migration along the southern New England shelf eastward in spring and westward in fall (Lux 1963). In the New York Bight, few were caught in summer. In March of this survey, the period of greatest gonad development, they were collected on the inner shelf at 9–68 m and 4.4–7.5°C (Table 1).

Winter flounder *Pseudopleuronectes americanus*

Highest mean GSI occurred during January in the estuarine survey area and during February in the ocean survey area (Fig. 15). Ripe females, 169–432 mm, were collected from September through April with 21% occurring in Raritan Bay. GSI declined rapidly after February; however, spawners were likely upriver beyond the range of this survey. Smith et al. (1975) captured larvae at inshore stations between the offing of Delaware Bay and Block Island Sound, Rhode Island from April through June, with spawning beginning in the south and progressing northward. Perlmutter (1947) reported spawning from December through May and concluded that the peak time varied with temperature. Pearcy (1962) found evidence of spawning from mid-February through April in the Mystic River estuary, Connecticut. Croker (1965) found winter flounder larvae in plankton collections in Sandy Hook Bay, New Jersey from April to June.

Although the water temperature at actual spawning sites is unknown, the average bottom temperature in Raritan Bay during January, the month of highest mean GSI, was 5.7°C. Of all the species encountered during this survey, winter flounder were collected in the coldest water.

Discussion

According to Braum (1978), most temperate zone fishes spawn in one of three generic seasonal patterns: spring, summer, or fall-winter. Based on the current study, alewife and yellowtail flounder are spring spawners; silver and red hake, black sea bass, butterfish, northern and striped searobin, and fourspot flounder are summer to fall spawners, while spotted hake and summer and winter flounder are fall-winter through early spring spawners. Offshore hake and windowpane belong to none of these groups, but appear to have protracted spawning seasons, i.e., these species' GSI were elevated, ovaries were ripe, and eggs and larvae were collected from spring through fall. Offshore hake inhabit the deeper waters of the Bight which are less influenced by changes in light and temperature. In contrast, windowpane inhabit the shallow, more seasonally influenced, inshore environs.

In temperate seas, there are distinct annual cycles of light intensity, temperature, nutrients, and winds

which drive cycles of productivity. An abundant source of food must be available for adult fish to produce stored fat for subsequent gamete production (de Vlaming 1972). Plankton of the right size, density, and quality must be available to pelagic larvae at the critical time of first feeding. As an example, the spawning of yellowtail flounder corresponds to the spring increase in zooplankton off southern New England (Sherman et al. 1984). The maximum concentration of zooplankton in the Middle Atlantic occurs from mid- to late-summer which coincides with the peak concentrations of larval searobins and butterfish as well as numerous other species (Sherman et al. 1984). The fishes that reproduce in the New York Bight during winter have already accumulated fat reserves during the summer and fall. Releasing eggs during winter may give a survival advantage to the larvae since many other fishes, potential competitors and predators, have migrated from the area and there is, therefore, little competition at a crucial time of development.

A short spawning season, represented by a steep GSI curve with a single peak, is a common strategy in temperate marine zones. Black sea bass, butterfish, and the searobins had the shortest spawning seasons, with ripe fish present for only 3–5 months. These four species are abundant during summer in the Middle Atlantic (Wilk and Silverman 1976ab, Wilk et al. 1977, Colvocoresses and Musick 1984), but not on the more boreal Georges Bank (Overholtz and Tyler 1985). They were collected at the highest average temperatures during their reproductive peaks (Table 1). Most of the other species described are abundant in both regions and were collected in colder waters.

Sherman et al. (1984) describe a ubiquitous or protracted spawning strategy for certain species including silver hake and *Urophycis* spp., in which eggs are produced for several months and, although mortality is high, some larvae survive when environmental conditions and food supply are properly matched. In this study, ripe female offshore silver and spotted hake, as well as windowpane, summer, and winter flounder, were collected for 5 or more months. Eggs and small larvae of these species were observed for many more months in other surveys (Clark et al. 1969; Smith et al. 1975, 1980; Colton et al. 1979).

Eggs are typically released from the ovaries of fishes in batches (Bagenal 1978). In species with short reproductive periods, these batches are released in the span of a few days with all individual fish spawning at about the same time. In multiple or serial spawners, batches of eggs mature and are shed several times during a long spawning season (Bagenal 1978, Burt et al. 1988). Examples of protracted spawners are silver hake which produce as many as three batches of eggs per spawning season (Fahay 1974) and summer flounder which produce up to six batches (Morse 1981). Summer flounder had the lowest mean GSI of any species collected during this survey, apparently because their eggs develop in batches and are released over an extended period. In contrast, the highest mean GSI noted were for yellowtail and winter flounder which produce only one batch of eggs per season (Howell 1983, Burton and Idler 1984). In both species, GSI increased gradually in fall through winter as eggs matured, with highest GSI levels being reached just prior to spring spawning. Similarly, Burton and Idler (1984) reported that GSI of winter flounder in Canadian waters gradually rose during the 8 months before spawning takes place in June.

A high GSI does not always parallel a high level of fecundity (Bagenal 1978). As an example, larger summer, yellowtail, and winter flounder have exhibited fecundities of over 1 million (Bigelow and Schroeder 1953, Morse 1981, Lux and Livingstone 1982); egg production in each of these species is accomplished, however, on different timetables.

Spotted hake and windowpane, both protracted spawners, had bimodal GSI curves. Various sizes of developing and ripe female spotted hake were collected in fall, while a few large ripe females were collected in spring. These findings may reflect behavioral differences among size or age classes, or perhaps the migratory habits of discrete unit stocks. Windowpane exhibited two GSI peaks in the New York Bight during 1974–75; however, continuous larval production throughout the summer was noted in an earlier survey of the area (Smith et al. 1975). Windowpane are permanent residents in the Bight; that is, no evidence of seasonal migration was found during this survey based on observed changes in abundance, size structure, or distribution of collections. Rather than a result of emigration, the bimodal GSI curve exhibited by windowpane may very well be a result of a reproductive tactic in which spawning is curtailed during the year if temperature rises above a preferred level.

Some of the most important and prolific commercial fisheries taking place in temperate seas around the world are based on families of fishes, such as gadids (codfishes and hakes) and pleuronectids (flounders), that are typically very fecund and produce relatively small pelagic eggs (Garrod and Horwood 1984). Of the species described in this study, the pleuronectids, yellowtail and winter flounder, and the bothid, summer flounder, have been reported to have extremely high fecundities. Such species are well-suited for commercial exploitation since they can recover rapidly from natural or man-induced depletion. The gadids described in this study are all small-bodied, mature early at a relatively small size, and produce many tiny pelagic eggs over a protracted spawning period; however, they

are not as fecund as larger and more robust gadid species such as Atlantic cod *Gadus morhua* (Hislop 1984).

A variety of reproductive strategies and tactics are used by the species to adapt to seasonal shifts in environmental parameters in the Middle Atlantic in general and the New York Bight specifically. In this way the entire region is continually used for reproduction by a wide range of economically and ecologically important species of resident and migratory finfish. These spawning adaptations contribute to the high diversity and abundance of finfish found in the Middle Atlantic region.

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Three New Species of Hagfishes, Genus *Eptatretus* (Cyclostomata, Myxinidae), from the Pacific Coast of North America, with New Data on *E. deani* and *E. stoutii*

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Abstract.—Three new species of the genus *Eptatretus*–*E. mcconnaugheyi*, from off Southern California and Northern Baja California, and an isolated population in the southern portion of the Gulf of California; *E. fritzi*, known only from the immediate vicinity of Guadalupe Island, Mexico; and *E. sinus*, confined to the midriff area of the Gulf of California—are described. New data are presented for *E. deani* and *E. stoutii*. A neotype is designated for *E. stoutii*.

Despite the extensive ranges of *E. deani* (southeastern Alaska to Guadalupe Island, Mexico) and *E. stoutii* (Vancouver Island, Canada, to Pt. San Pablo, about 80 miles southerly from Cedros Island, Mexico), no appreciable differences were found in counts and body proportions within each species. However, the disjunct populations of *E. mcconnaugheyi* display significant differences ($P>0.001$) in numbers of trunk and total slime pores; in all other characters the two populations are very similar.

Sex ratios for four of the species are notably uneven, ranging between 60% and 74% female, 26% and 40% male. The sex ratio for *E. stoutii* is essentially even, 49% female and 51% male.

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This study continues our efforts on the genus *Eptatretus*, a part of the unfinished work of Carl L. Hubbs (deceased 30 June 1979). Two previous studies (McMillan and Wisner 1984, Wisner and McMillan 1988) and this have resulted in descriptions of seven new species of *Eptatretus*, two from off Central Chile, one each from the Hawaiian and Philippine areas, and three herein. Also, we have described a new species, *Nemamyxine kreffti*, from off Rio de Plata, Argentina (McMillan and Wisner 1984). In addition, a study on the genus *Myxine* is progressing, involving at least six new species from off the Atlantic and Pacific coasts of North and South America.

The present effort includes the largest amount of study material, about 2300 specimens. Many specimens of *E. stoutii* and *E. deani* are not included in the lists of material examined due either to poor preservation, to questionable capture data, or to a surfeit of material from an area, particularly off southern California. All specimens from near the extremes of ranges are included, as are all specimens of the three new species.

Due to the availability for the first time of large numbers of specimens of *E. stoutii* and *E. deani*, each having extensive distributions, we attempted to delineate an annual and spatial period of deposition (extrusion) of eggs for each. Capture data for females containing eggs of at least 20 mm length showed that eggs of this size were present in both species throughout the year throughout all areas of their ranges. The maximum lengths of eggs were 28.6 mm for *E. stoutii* and 52.3 for *E. deani*. Although these lengths may not indicate the ultimate lengths of eggs at time of deposition, it is very probable that deposition by both species occurs throughout the year and in all areas of their distributions.

Except for two collected in November, all specimens of *E. fritzi* were taken in April; eggs to 33 mm were present. Similarly, specimens of *E. sinus* were taken within two short periods, 20–22 January and 28 February–2 March eggs to 32 mm were present.

The occurrence and arrangement of head grooves (lateral lines of authors) in all species treated here agree well with those described and figured by Ayers and Worthington (1907:332–333, figs. 5, 6) and by McMillan and Wisner (1984:255, fig. 4).

Methods and materials

Methods of counting and measuring are those recommended by McMillan and Wisner (1984) and Wisner and McMillan (1988). Features used in

Figure 1

Outline of hagfish (*Eptatretus*) showing regions and features used in measuring and counting: A–H, total length (TL); A–B, prebranchial length; B–C, branchial length, including gill apertures (GA); D, external opening of pharyngocutaneous duct (PCD); E, ventral finfold; C–F, trunk length; F, origin of cloaca; F–H, tail length; G, caudal finfold. The linear series of dots represents the prebranchial, branchial, trunk, and cloacal-caudal (tail) slime pores.

counting and measuring are shown in Figure 1. Abbreviations used are given below and identified in Figure 4.

Abbreviations

ABA Afferent branchial artery; one of the small blood vessels that lead to each gill pouch from VA or its branches (Fig. 4).

DM Dental muscle; the firm elongate, cylindrical complex of muscles and cartilages that moves the dental plates and sets of cusps during feeding. Posterior portions of DM are shown in Figures 2–4, lying between rows of gill pouches.

GA Gill (branchial) aperture; external opening of the efferent duct leading from a gill pouch (Fig. 1).

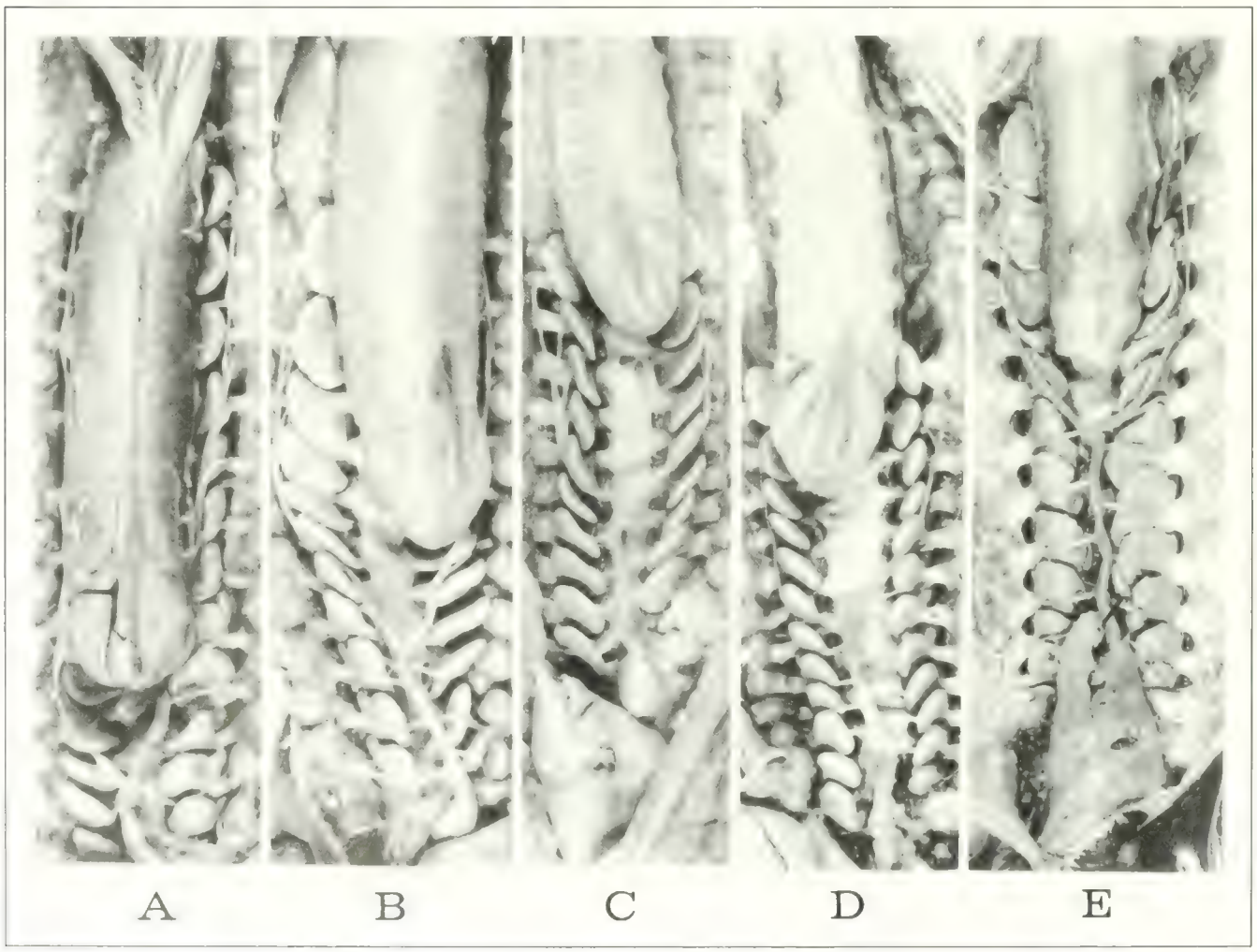
GP Gill pouch; rounded, serially arranged structures along and posterior to the dental muscle (Fig. 4).

PCD External opening of the pharyngocutaneous duct; always confluent with the posteriormost left gill aperture in most species of *Eptatretus*, and much larger than all other apertures (Fig. 1).

VA Ventral aorta; the portion between the heart (ventricle) and to where it branches to each side of DM (Fig. 4).

Figure 2

Branchial areas of holotypes of (A) *Eptatretus mcconnaugheyi*, (B) *E. fritzi*, and (C) *E. sinus*; (D) neotype of *E. stoutii*; (E) *E. deani*. The dental muscle (DM) is the cylindrical mass lying between the rows of gill pouches (GP).



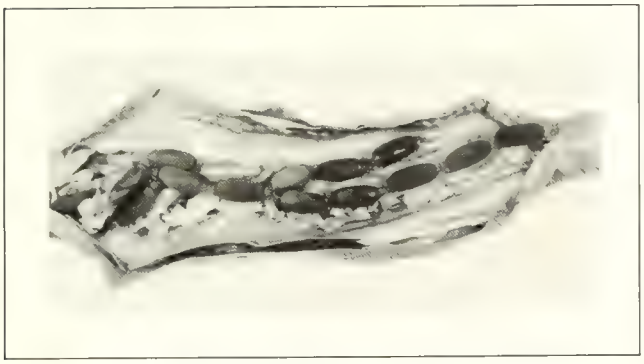


Figure 3
Mature eggs of holotype of *E. mcconnaugheyi* showing *in situ* arrangement and connections by anchor filaments (terminal hooks).

Other features used are:

Preocular length From center of left eyespot to center of rostrum.

Barbel length From crease at mesial base to tip of barbel.

Collection data and deposition of specimens are listed for each species. All specimens were taken on bottom, with a trap or trawl, except for two of *E. stoutii* taken by scuba divers near San Diego. Institutions which have provided study material, or in which type specimens are deposited, are SIO, CAS, LACM, MCZ, USNM, OSUO, BCPM, and UW. These symbolic institutional codes follow the usages in Leviton et al. 1985.

We introduce length of barbel as a systematic character. Barbels have not been used in the taxonomy of hagfishes except for the presence, absence, or degree of pigmentation between bases and tips. No tabular comparison of lengths has previously appeared in print, perhaps due to the small numbers of specimens available. However, in this study a total of 2613 measurements of length of first nasal barbel, left side, provided material for comparison. Data in Table 6, first barbel length for 25-mm increments of total length, show significant differences in lengths within the five species treated.

Key to species of *Eptatretus* of the Pacific coast of North America

1a Prebranchial length usually less than branchial length, very rarely equal to or even slightly greater. Tail length always less than branchial length ..... ***E. mcconnaugheyi* n. sp.**

1b Prebranchial and tail lengths always greater than branchial length 2

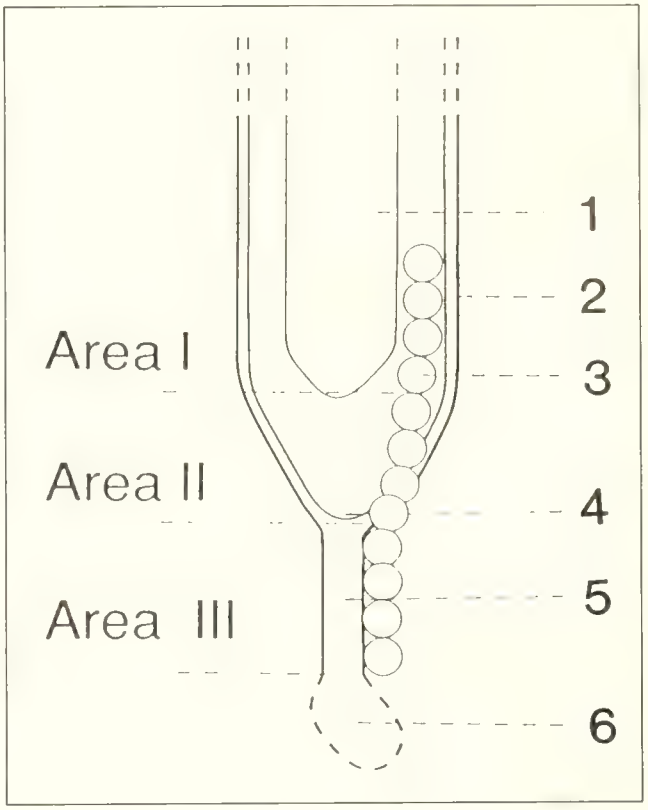


Figure 4
Sketch of branchial area, ventral view, of a hagfish (*Eptatretus*) delineating Areas I, II, and III, referred to in counts of gill pouches for each Area given in Table 8. (1) DM, posterior portion; (2) left branch of VA; (3) gill pouch; (4) point of branching of VA; (5) VA; (6) ventricle.

2a Prebranchial slime pores 7(4–10). Ventral finfold weakly developed, often vestigial or absent. Barbels small, not robust. Color dark purplish brown ..... ***E. deani***

2b Prebranchial slime pores 12–17. Ventral finfold variably well developed to absent. Barbels variably large to small. Color purplish to light or dark reddish brown 3

3a All barbels large, robust. Third barbel 49%(42–59%) of preocular length. Prebranchial slime pores 12–13(10–15). Branchial apertures 11(10–12). Ventral finfold very weakly developed, usually absent. Color dark purplish brown..... ***E. fritzi* n. sp.**

3b All barbels small, not robust. Third barbel 34%(31–37%) of preocular length. Prebranchial slime pores 13–17. Ventral finfold either prominent, vestigal or absent. Branchial apertures 10–14. Color dark brown to light reddish brown 4

4a Branchial apertures 12(10–14). Ventral finfold prominent, with wide pale margin. Color light reddish gray or light brown. Extensive piebaldness common ..... ***E. stoutii***

4b Branchial apertures 10(9–12). Ventral finfold vestigial or absent. Color dark reddish brown, not piebald ..... ***E. sinus* n. sp.**

Systematics

Eptatretus mcconnaugheyi new species

It is not feasible to attempt a meaningful synonymy for this new species, as it and *E. stoutii* are very similar and occur sympatrically off southern California. *Eptatretus stoutii* has long been extensively used in biochemical and physiological research. However, none of this research material has been examined by us, and no identification credited to competent ichthyologists. As *E. mcconnaugheyi* is not previously known, it is very likely to have formed a part of this research material, particularly from southern California.

Holotype SIO69-231E, female, 482 mm TL, taken at 32°32′0″N, 117°21′07″W, in a trap on bottom at 148 m, 11–12 April 1969.

Paratypes SIO69-228B, 14(185–400 mm TL), taken at 32°05.9′N, 117°04.4′W, 177 m, 10–11 March 1969; SIO71-114, 7(360–440 mm TL), taken at 28°21.0′N, 115°43.0′W, 689 m, 25–26 May 1971; SIO69-231E, 7(200–448 mm TL), taken with the holotype; SIO68-126, 5(355–409 mm TL), taken at 25°49′N, 110°51′W, 351 m, 25–26 January 1968; CAS 63203, 7(210–400 mm TL), taken at 32°31.8′N, 117°21.6′W, 145 m, 29 September 1972; LACM 44409-1, 6(195–430 mm TL), taken at 32°31.8′N, 117°21.1′W, 145 m, 29 September 1972; USNM 29630, 7(245–380 mm TL), taken at 32°31.8′N, 117°21.1′W, 145 m, 29 September 1972.

Additional material SIO56-9, 1(340), 42 m; SIO68-109, 1(390), 415 m; SIO68-11, 1(230), 177 m; SIO68-124, 1(249), 205 m; SIO68-125, 19(239–347), 278 m; SIO68-126, 5(355–409), 351 m; SIO68-127, 3(315–440), 238 m; SIO69-179, 2(235–376), 109 m; SIO69-181, 2 (141–312), 183 m; SIO69-225C, 1(392), 371 m; SIO69-228B, 14(195–406), 99 m; SIO69-228C, 1(433), 166 m; SIO69-231C, 1(372), 139 m.

Distribution *Eptatretus mcconnaugheyi* appears to consist of two disjunct populations: one from Santa Monica Bay, California, to the Cedros and San Benito Islands, Mexico, and one apparently restricted to the lower portion of the Gulf of California. These two populations appear to differ significantly ($P>0.001$) in numbers of trunk and total slime pores, the higher counts occurring in the southern California population.

Depths of capture range between 42 and 384 m off southern California and between 177 and 415 m in the Gulf of California. Collecting efforts between the Cedros and San Benito Islands and the mouth of the Gulf have failed to take the species.

Diagnosis Prebranchial length usually less than branchial length, rarely equal to or very rarely even slightly longer. Body moderately robust, deepest at midbody, its width about half its depth, increasingly laterally compressed toward tail. Tail length 13–16% of TL, its depth about half its length. Ventral finfold usually prominent, often low, with pale margin. Caudal finfold prominent, wide, the margin thin and pale. Three fused cusps (multicusp) on anterior, two fused cusps on posterior, set of cusps.

Etymology We take great pleasure in dedicating this new species to Ronald R. McConnaughey, friend and superb marine technician, who was instrumental in the development of capture gear and party to the collecting of many of the thousands of specimens of species examined by us.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated here. Body moderately robust, deepest at midbody, the width about half the depth, increasingly laterally compressed toward tail. Tail spatulate, its length about twice its depth, its ventral margin sloping downward below level of body. A thin, deep caudal finfold, with a narrow pale margin, extends from cloaca around end to about over cloaca dorsally. Ventral finfold low, usually entirely unpigmented. Head at eyespots about as deep as wide, narrowing to rostrum. Width of rostrum about half the width of head at eyespots. Eyespots rather prominent, of moderate size, the margins well defined. Oral surface short, sloping posteriorly at about 45° angle from the vertical. Barbels small, the distal thirds unpigmented. First barbel only slightly shorter than second, often equal to or slightly longer, averaging 64%(52–79%) of length of third, the second barbel averaging 70%(51–84%) of length of third. Length of first nasal barbel, left side, is given in Table 6 and compared with that of other species treated.

Head grooves Grooves present before and behind eyespots on each side of dorsal midline. Three to six grooves, each side, before eyespots lie in longitudinal rows, and two to four ventrad in transverse rows. One to eight grooves may occur behind eyespots. Most lie transversely, with none to three longitudinally, at sides. As many as 24 grooves may occur on one specimen.

Color a dark, reddish brown in life without pale spots or areas. Barbels pale on distal thirds.

Length of DM 27%(21–39%) of TL. DM width 68% (57–90%) of its depth. VA variable in length, averaging 11%(5–22%) of DM length. DM to VA 14%(5–26%) of DM length, and 1.4%(0.5–9%) of VA length. Number of GP in positions relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species discussed herein. Afferent duct of last GP, left side, always confluent with PCD.

Higher numbers of GA, left vs. right sides, may differ between the two populations (Table 8). Off southern California, the higher count is about equal for both sides at 4 and 5 each. In the Gulf population, the higher count is always on the left side.

Eggs The holotype contains 18 mature eggs, the largest 25.2 × 9.0 mm. The largest egg found in any female is 26 × 8 mm. The smallest female with eggs, most in round or slightly ovoid stages, is 267 mm TL. It may be that females of the Gulf population mature at a smaller size than do those from southern California. One, 267 mm TL, has eggs to 15.8 mm; one, 352 mm TL, has eggs to 20.8 mm; and one, 32 mm TL, has eggs to 17.6 mm. These figures contrast sharply with those of the southern California population, in which eggs ranging between 15 and 29 mm occur only in females of 400–508 mm TL. Perhaps these differences are an artifact of sampling or of developmental stages relative to both time and size, or to the relatively small number of specimens available (97).

All mature eggs of the holotype have fully developed anchor filaments (terminal hooks) with most free of encapsulating membrane (Fig. 3), and apparently ready for extrusion. This condition was rarely observed among the nearly 2400 specimens of all species of *Eptatretus* examined by us in the course of our studies. The eggs are linked by filaments in rows in a fashion similar to that shown by Dean (1989) and Jensen (1966).

The sex ratio is unbalanced. Of a total of 58 specimens for which sex could be reliably determined, 64% were female and 36% male.

Differentiation All body proportions and most counts for the two disjunct populations are very similar. However, significant differences ($P>0.001$) occur in numbers of trunk and total slime pores (Tables 3, 4), despite considerable overlap in values of thousandths of total length.

Discussion This species and *E. stoutii* appear to be closely related and occur sympatrically off southern California. However, the two are readily separable in that the prebranchial length of *E. mcconnaugheyi* is less, rarely even slightly longer, than the branchial length, and always greater in *E. stoutii*. Also, the numbers of prebranchial slime pores differ notably, 8–9 (6–11) in *E. mcconnaugheyi* and 13(10–16) in *E. stoutii* (Table 2).

Eptatretus fritzi new species

Holotype SIO66-26, male, 550 mm TL, taken at 28°51′N, 118°14′W, in a trap on bottom at 512 m, 3–4 April 1966.

Paratypes SIO66-26, 30(280–585 mm TL), taken with the holotype; CAS 63201, 15(325–540 mm TL), taken with holotype; LACM 44407-1, 15(375–495 mm TL), taken with the holotype; USNM 296318, 15(350–570 mm TL), taken with the holotype; SIO63-177, 20 (324–522 mm TL), taken at 28°52′N, 118°14′W, 2743 m, 24 April 1963; SIO66-22, 36(232–521 mm TL), taken at 29°06′N, 118°17′W, 402 m, 12 April 1966; SIO66-23, 195(286–556 mm TL), taken at 28°54′N, 118°13′W, 444 m, 2–3 April 1966; SIO66-36, 2(354–405 mm TL), taken at 29°30′N, 117°17′W, 512 m, 6–7 April 1966; SIO67-60, 120(281–498 mm TL), taken at 29°09′N, 118°16′W, 832 m, 26–27 April 1966; SIO68-664, 2 (425–535 mm TL), 183 m, 15–16 November 1968; SIO72-294, 4(207–541 mm TL), taken at 29°10′N, 118°16′W, 256 m, 12–13 April 1970.

Distribution Known only from the immediate vicinity of Guadalupe Island, Mexico. Depths of capture range between 182 and 2743 meters.

Diagnosis All barbels notably larger and more robust than on any other species of *Eptatretus* known to us (Table 6). Ventral finfold absent or vestigial, without pale margin. Prebranchial and tail lengths each greater than branchial length. Color a dark purplish-brown. Prebranchial slime pores 12(10–15). Three fused cusps (multicusp) on anterior set of cusps, two fused cusps on posterior set.

Etymology We take great pleasure in dedicating this species to Frithjof (Fritz) Ohre, friend, willing, eager, and industrious volunteer on many of the expeditions on which all species treated here were taken, particularly those to Guadalupe Island.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated here. Body robust, deeper than wide, deepest at midbody, increasingly laterally compressed toward tail. Tail spatulate, its depth about half its length, its ventral outline not sloping downward from cloaca. Caudal finfold variably

thin to thick, beginning at cloaca and extending around tail to about over origin of cloaca, without pale margin. Ventral finfold usually absent, present in only 28 of 341 specimens (8.2%). When present it is intermittently and weakly developed along its length. It is thick, heavy, and without pale margin.

Head at eyespots about as deep as wide, narrowing to rostrum. Eyespots prominent, the margins irregular. Oral surface sloping posteriorly at about a 35° angle from the vertical. All barbels are notably longer and thicker in proportion to total length than on any other myxinid known to us (Table 6). First and second barbels about equal in length, the third averaging 49%(42–50%) of preocular length. First barbel as long or longer than width of nasal orifice when manually flattened (124%(100–203%)). First barbels average less than 50% of this width in all other species of *Eptatretus*.

Head grooves Grooves always present behind eyespots but occasionally absent before. Those behind average 5(3–10) in number and are arranged mostly in transverse rows with an occasional few grooves lying ventrad and longitudinally. Those before eyespots average 3(1–6) in number and lie longitudinally. Grooves behind eyespots originate very near the dorsal midline but do not cross. Those before eyespots are notably more distant from the midline.

Color Color a dark purple to black in most specimens, a chocolate brown in others, rarely showing pale spots. Notes by the senior author, party to the first and most subsequent captures, state, "a dark color." The chocolate color may be an artifact of preservation. GA, slime pore margins, and ventral finfold are without pale margins.

DM short, moderately robust, its length 27%(21–34%) of TL. DM width 13%(11–15%) of its length, its depth 73%(58–88%) of its width. VA length variable, 16%(8–42%) of DM length. DM to VA also variable, 15%(4–32%) of DM length and 90%(24–206%) of VA length. Numbers of GP in positions relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species treated here. Afferent duct of last GP, left side, always confluent with PCD.

Variation occurs in numbers of GA between left and right sides, the higher number always on the left side, 81 vs. 0 instances (Table 8).

Eggs The largest egg, 33.8 × 8.5 mm, occurred among 14 large eggs in a 386-mm TL female. No more than 16 and as few as 10 almost fully developed eggs were found in any female. No egg had free anchor filaments, but occasionally they were visible through the encapsulating membranes.

The sex ratio is unbalanced. Of a total of 358 specimens for which sex could be reliably determined, 60% are female and 40% male.

Discussion This species and *E. deani* occur sympatrically near Guadalupe Island, Mexico. Both were taken in the same trap on two occasions. They are similar in coloration, being very dark brown to purplish-black, but *E. fritzi* seems much less prone to piebaldness than *E. deani* as very few pale spots were noted. Primary differences are that the barbels of *E. fritzi* are much longer and more robust than those of *E. deani* (Table 6), and that it has more prebranchial pores, 12 (10–15) vs. 7(4–10). Also, *E. fritzi* usually has no ventral finfold (313 of 341 specimens, 91.8%), whereas in *E. deani* this finfold is usually present (863 of 892 specimens, 96.6%), although rather weakly developed.

Eptatretus sinus new species

Holotype SIO68-108, female 307 mm TL, taken at 25°49′N, 110°44′W, in a trap on bottom at 708 m, 22–23 January 1968.

Paratypes SIO68-108, 31(230–425 mm TL), taken with the holotype; SIO68-94, 29(129–346 mm TL), taken at 29°20′N, 113°10′W, 263 and 283 m, 20 January 1968; SIO68-100, 60(267–464 mm TL), taken at 29°00′N, 113°25′W, 467 m, 20–21 January 1968; CAS 63202, 15(270–400 mm TL), taken at 25°49′N, 110°44′W, 708 m, 22–23 January 1968; LACM 44408-1, 14 (270–400 mm TL), taken at 25°49′N, 110°44′W, 708 m, 22–23 January 1968; USNM 296319, 15(275–420 mm TL), taken at 25°49′N, 110°44′W, 708 m, 22–23 January 1968.

Additional material SIO68-97, 7(223–308), 881 m; SIO68-98, 17(276–338), 881 m; SIO68-99, 11(263–420), 668 m; SIO68-101, 16(264–355), 198 m; SIO69-201, 1 (190), 1454 m; SIO69-203, 11(381–630), 759 m; SIO69-206, 54(363–430), 768 m; SIO69-207, 57(259–404), 475 m.

Distribution Known only from the midriff area of the Gulf of California, Mexico, between about 28° and 30°N latitudes. Depths of capture range between 198 and 1330 meters.

Diagnosis Prebranchial length greater than branchial length. Tail length usually greater than branchial length, occasionally equal to or less. Ventral finfold low, unpigmented, occasionally absent. Barbels usually unpigmented, except rarely at bases. Three fused cusps (multicusp) on anterior, two fused cusps on posterior, sets of cusps.

Etymology From the Latin "sinus," meaning gulf, by reason of its apparent restriction to the midriff area of the Gulf of California, Mexico.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated here.

Body robust, deepest at midbody, deeper than wide, increasingly laterally compressed toward tail. Tail spatulate, its depth about half its length, its ventral outline not sloping downward from cloaca. Caudal finfold thickened ventrally, thinner around tail, ending dorsally over cloacal origin. Ventral finfold usually present, low, unpigmented. It is absent on 10% of 363 specimens.

Head at eyespots as deep as wide, the oral surface sloping posteriorly at about 35° from the vertical. Eyespots prominent, the margins well defined. Barbels short, unpigmented except rarely at bases. Second barbel usually longer than first but occasionally shorter or of equal length. First and second barbels respectively 60% and 64% of third barbel. Length of first nasal barbel is given in Table 6 and compared with that of other species treated.

Head grooves Grooves present before and behind eyespots, each side. One to five grooves occur behind eyespots, most lying transversely, but a few lying longitudinally at side of head. One to four grooves lie before eyespots in longitudinal rows. Occasionally no grooves occur before eyespots.

Color Color reddish-brown, without pale markings or spotting. GA, PCD, and an occasional slime pore have narrow pale margins.

Length of DM 24%(21–29%) of TL. DM width 14% (12–17%) of its length, its depth 65%(54–86%) of its width. DM to VA 16%(15–26%) of DM length. VA length 25%(17–39%) of DM length. VA length variable, averaging 66%(22–127%) of distance from DM to VA. Numbers of GP in position relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species treated here. Afferent duct of last GA, left side, always confluent with PCD.

Variation in numbers of GA occurs between left and right sides, with higher numbers predominating on the left, 65(15%) vs. 8(2%), N 444 (Table 8).

Eggs The holotype, 370 mm TL, contains many small eggs, to about 4 mm. The largest egg found (among 21 large ones) was 32 × 7.5 mm in a female of 371 mm TL. The most eggs found was 37 (18 × 5 mm) in a female of 420 mm TL. Eggs (28) to 21 mm were found in a female of 372 mm TL, and to 23 mm in one of 335 mm TL. Apparently, *E. sinus* matures at a short total length, as a male of 130 mm and a female of 142 mm were noted. These are surprisingly small sizes, for in other species, these total lengths are distinctly juvenile, and the sex determinable only under very high magnification, if at all. Encapsulated anchor filaments are visible on eggs of 20 mm length.

The sex ratio of *E. sinus* is unbalanced. Of a total 424 specimens for which sex was reliably determined, 65% are female, 35% male.

Eptatretus deani (Evermann and Goldsborough 1907)

Synonymy

Polistotrema deani Evermann and Goldsborough 1907: 221–222, 225–226, fig. 1 (original description; compared with *Polistotrema stoutii*; Albatross Station 4235, Spacious Bay, Cleveland Peninsula, 130–193 fathoms, and Albatross Station 4238, Nose Point, Behm Canal, southeastern Alaska, 229–231 fathoms); Wilimovsky 1954a: 3, and 1954b: 281 (SE Alaska to California), 1958: 18 (compared with *P. stoutii*; SE Alaska to California); Barham et al. 1967: 780, fig. 7 (shown associated with *Anoplopoma fimbria*, Trieste Dive 105; 1060 m in San Diego Trough) [presumptive].

Polistotrema curtiss-jamesi Townsend and Nichols, 1925: 4–5, 18, 20, fig. 1 (original description; compared with *P. stoutii*; south of Monterey to Santa Barbara I.: 440–585 fathoms; Albatross Stations 5695, 5696, 5697, 5698; type locality Station 5697, 585 fathoms).

Heptatretus deani Regan, 1912: 534–535 (comparisons; synonymy; references; diagnosis; Alaska).

Bdellostoma deani, Adam and Strahan 1963; 6 (11–12 gills; length to 620 mm; Alaska).

Eptatretus deani, Day and Pearcy 1968: 2668, 2771 (listed; about 1200 meters off Oregon); Bourne and McAllister 1969: 3246–3248, fig. 1 (first British Columbia records, 54°47′N, 130°58′30″W at 90–250 fathoms: 48°53′N, 126°40′W at 373 m: description); Kukowski 1972: 7, 24 (Monterey Bay; references); Miller and Lea 1972: 32 (Cedros and Guadalupe Is., Baja California to SE Alaska: length to 20 inches; depth 1560–3500 feet; common in deep water, uniform purplish black); Fitch 1973; 815 (off Eureka, California, 565–585 m); Hart 1973: 10, 16–18, fig. 1 (first description for Canada; comparisons in key; description; geographical and bathymetric distributions; references); Gates and Frey 1974: 60 (vernacular, California); Smith and Hessler 1974; 72–73 (14 miles off San Diego; depth 1230 m; respiration rate measured *in situ*; a dominant species in San Diego Trough); Jespersen 1975: 189–190, 195, 197,

fig. 15 (spermiogenesis; southern California off San Clemente I. at about 1280 m; off Los Coronados I. at about 1097 m; Theisen 1976: 167–173, figs. 2. 4. 7. 10 (microstructure of olfactory system; southern California; 1097 m.

Holotype USNM 57820, sex not determined, "21" inches (about 535 mm TL), taken near Yes Bay, Behm Canal, Cleveland Peninsula, southeastern Alaska, easterly of Ketchikan, about 55°55′N, 131°55′W, by dredge at 419–423 m (Albatross Station 4238), 8 July 1903.

Paratypes USNM 61162, two: one a female, in rotting condition, taken at Albatross Station 4229 and 4235, Behm Canal, southeastern Alaska, Nose Point, near the holotype, by dredge at 419–423 m, 16 July 1903. (The type specimens were examined by Carl L. Hubbs at USNM, 25 February 1972.)

Additional material SIO59-47, 6(359–458), 823 m; SIO60-540, 1(484), 1920 m; SIO63-177, 20(286–457), 2743 m; SIO63-868, 21(345–498), 107 m; SIO64-281, 1(451), 587 m; SIO64-496, 5(374–455), 475 m; SIO64-497, 26(335–445), 512 m; SIO64-498, 37(291–441), 616 m; SIO64-499, 38(294–473), 960 m; SIO65-499, 54 (321–521), 933 m; SIO65-465, 19(370–554), 1302 m; SIO66-27, 2(148–455), 1252 m; SIO66-36, 130(233–509), 512 m; SIO66-535, 21(377–453), 1013 m; SIO66-537, 1(417), 1244 m; SIO66-551, 2(390–401), 1156 m; SIO67-64, 20(380–510), 980 m; SIO67-109, 52(312–523), 1024 m; SIO67-110, 1(369), 1445 m; SIO67-118, 51(288–467), 732 m; SIO68-427, 5(396–470), 1840 m; SIO68-428, 6(320–481), 800 m; SIO69-225F, 38(342–429), 633 m; SIO69-227B, 26(288–495), 744 m; SIO69-288D, 56(182–423), 609 m; SIO71-103, 4(401–484), 1373 m; SIO71-7, 42(280–484), 1244 m.

The following collections, with incomplete data were taken between British Columbia and northern California: OSUO 3869, 3(267–450), OSUO 3870, 2(385–415), OSUO 3871, 2(404–447), BCPM 46-15, 1(366), BCPM 72-9, 4(402–475), BCPM 72-10, 1(460), CAS 10877, 1(390), CAS 26633, 2(318–365), CAS 20404, 1(395), Albatross Station 3126, 1(317), 378 m; UW 00379, 1(440), 155 m; UW 18148, 1(391), 595 m; UW 18149, 1(383), 1098 m; UW 18151, 1(405), 1190 m; UW 18152, 7(370–445), 1190 m; UW 18153, 2(402–466), 932 m; UW 18154, 1(354), 183 m; UW 18155, 6(376–433), 1190 m; UW 18157, 5(400–440), 732 m; UW 18158, 12(342–459), 824 m; UW 18159, 2(343–375), 732 m; UW 19095, 3(421–440), UW 19127, 2(414–444), UW 19206, 1(320), UW 19310, 6(382–479).

Distribution Southeastern Alaska to near Guadalupe Island, Mexico. Despite this extensive range of about 2600 miles, no significant variation in counts or measurements with latitude was demonstrated.

Diagnosis Prebranchial slime pores 7(4–10). Prebranchial length usually greater than branchial length, rarely equal to or less. Tail length variably equal to, or slightly less or greater than branchial length. Color a purplish-black, with occasional pale spots and areas. Anterior part of head often pale. Three fused cusps (multicusp) on anterior set of cusps, two fused cusps on posterior set.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated here.

Body robust, deeper than wide at midbody, progressively laterally compressed toward tail. Prebranchial slime pores 7(4–10). Branchial apertures 11(10–12). Prebranchial length usually greater than branchial length, rarely equal to or less. Tail length greater than branchial length in 45%, equal-to in 30%, and less-than in 26% of 441 specimens. Ventral finfold weakly developed, occasionally absent, without pale margin. Tail spatulate, its ventral surface sloping downward at a slight angle from the ventral body line. Head wider than deep. First barbels usually shorter than second, occasionally equal to or slightly longer; the first about 58% of length of third barbel, the third about 70% of preocular length. Eyespots prominent, variable in size, usually with irregular margins. Length of first nasal barbel is given in Table 6 and compared with that of other species treated.

Head grooves Of 104 specimens selected for mucus-free condition, 18 (17%) had no grooves. Of those having grooves before eyespots, 45% had them on both sides, about 6% had them on either the right or left side only. Grooves occur on both sides behind eyespots in 80%, on the left only in 8%, and on the right side only in 12% of the 104 specimens.

Color Color usually a purplish-black or very dark brown. Specimens with a brownish base color show variable amounts of pale spots and patches (piebaldness) that range from slight to considerable. An occasional specimen has a pale head from rostrum to first few prebranchial slime pores. Most heads are pale near tip of rostrum. On pale heads, the barbels usually are unpigmented. Ventral and caudal finfolds without pale margin except when spotted in piebald specimens. Gill apertures and slime pores with narrow pale margins. Cloacal margins with rather wide pale areas.

Variation occurs in numbers of GA between left and right sides with higher numbers predominating on the left, 125 (11%) vs. 21 (2%) on the right side in 1145 counts (Table 8).

DM length 24% (20–26%) of TL. Width of DM 15% (13–18%) of its length, its depth 64% (54–80%) of its width. DM to VA 9% (0–15%) of DM length. VA length 31% (23–36%) of DM length. Numbers of GP in positions relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species treated herein. Afferent duct of last GA, left side, always confluent with PCD.

Eggs Mature eggs large, usually distinctly curved. The largest egg found measured 52.3 × 10.5 mm and was among 14 large eggs in a 500-mm TL female. Apparently very few eggs mature at one time from the many hundreds of tiny, round to slightly ovoid eggs normally present. No more than 15 nor fewer than 8 large eggs (30 mm and longer) were present in any female. Anchor filaments were visible on all eggs of 35 mm length or more, but were still encapsulated.

The sex ratio of *E. deani* is notably unbalanced. Of a total of 480 specimens, 74% were female, 26% male. The smallest female noted was 249 mm TL, the smallest male 255 mm TL.

Eptatretus stoutii (Lockington 1878)

Synonymy The following synonymy includes only those references arbitrarily considered by us to have taxonomic, behavioral, or distributional value and not mere usage of the name. About 120 references using the name *stouti* or *stoutii* pertain only to biochemical and/or physiological studies that serve no apparent taxonomic purpose and are not included.

Bdellostoma stoutii Lockington, 1878:792–793 (original description; compared with *B. polytrema*; mouth of Eel River, Humboldt County, California); Jordan and Gilbert 1883:6 (brief description, after Lockington; coast of California; not rare).

Bdellostoma stouti, Dean 1899:223–276 (embryonic development of larvae and eggs).

Bdellostoma dombeyi, Jordan and Gilbert 1883:57 (in part; characters and feeding habits; California); Worthington 1905:625–663 (description, behavior in aquaria; habitat in Monterey Bay; counts of gill openings; feeding; eggs); Ayers and Worthington 1907: 327–336 (figures and description, lateral lines found only on head).

Homea stoutii, Dean 1903:295–298 (partial albinism in anterior portion), 1904: 6. 7. 16, 18, 20 (seasonal spawning; largest are females; California).

Heptatretus stouti, Regan 1912:534–535 (synonymy; comparisons; diagnosis; California).

Eptatretus stouti, Starks and Morris 1907:161 (common in deep water off San Diego; north to Cape Flattery; abundant in Monterey Bay); Strahan 1963:22 (behavior and attitudes in aquaria); Linthicum 1971: 17–22 (immunological study; tying itself in knots to remove slime; slime production, teeth); Kukowski 1972:24, 37, 43 (Monterey Bay and Elkhorn Slough; references), 1973:7, 19, 22–23 (Monterey Bay; occurrence data; recurrent groupings); Anonymous 1973: 68 (observed at camera station at 306 m, SW of White's Point, southern California); Allen 1976:95 (only species not taken in otter trawl or by setline in Santa Monica Bay, southern California; has been so collected elsewhere); Downing et al. 1981:326–328 (description and figures of mucus thread cells in slime glands); Fernholm 1985:113–122 (in part; no ciliated cells or innervation or electroreceptory capacity found in lateral lines).

Polistotrema stouti, Clemens and Wilby 1946:9 (characters; white margin on ventral finfold; reaches 25 inches; species attacked; attachment of eggs; W coast, Vancouver I.).

Polistotrema stoutii, Fowler 1908:461 (Pacific Grove on Monterey Bay, California; gill opening counts for 8 specimens); Clemens and Wilby 1961:18, 49–50 (description; history on British Columbia west coast; eggs; southern California to SE Alaska; in part); McInerney and Evans 1970:966–968 (habitat characteristics; Mayne Bay in Barkley Sound, Vancouver I.); Sasaki 1972:283 (Queen Charlotte Sound, Vancouver I.; rare).

Dodecatrema stoutii, Fowler 1947:3 (proposed new name to replace *Bdellostoma*).

Eptatretus stoutii, Jensen 1959:798 (albino and piebald variants; ratio to normal; habitat; abundance in southern California; submarine canyons tributary to San Diego Trough; 210 fathoms), 1966:82–90 (habits; description and figures of the four hearts; functions); Taylor 1967:181–187 (chromosome numbers; probably supernumeraries; Alaska to Baja California; habitat; 60–1800 feet); Day and Pearcy 1968:2668 (depth distribution off Oregon); Bourne and McAlister 1969:3248 (compared with *E. deani*); Miller and Lea 1972:32 (Pt. San Pablo, Baja California, to SE Alaska; length to 25 inches; depth range 30–2400 feet; description); Hart 1973:16, 18–19, 53 (comparisons in key; description; common; geographical and bathymetric distribution in and off Barkley Sound; probably quite generally distributed in British Columbia; Alaska records not confirmed in recent reviews; references; egg cases); Smith and Hessler 1974:72–73 (*in situ* respiration rate significantly greater than that of *E. deani*); Anonymous 1974:50 (observed only during day at baited camera off Palos Verdes, California); Fernholm 1975:201–203 (structure and deposition of eggs compared with that of *E. burgeri*; *Bdellostoma dombeyi* of Worthington referrable to *E. stoutii*); Jespersen 1975:189–198

(spermiogenesis; offshore in 45.7 and 53.0 m); Knaggs et al. 1975:56–57 (taken off central Baja California; southern range extended from Cedros I. to Pt. San Pablo); McMillan and Wisner 1984:255 (lateral line described and figured); Wisner and McMillan 1988:231 (the term "head grooves" suggested to replace that for lateral lines.

Neotype SIO68-426, male, 530 mm TL, taken about 2 miles southwest of the whistler buoy at entrance to Humboldt Bay, California, in a trap on bottom at 38–44 m, on 27 August 1963.

Additional material, northernmost collections SIO 68-426, 34(291–527), taken with the neotype. BCPM 60-1, 2(474–580), taken at about 49°33′N, 126°38′W, outside Nootka Bay, Vancouver I.; no other data; BCPM50-3, 2(192–420), taken off west coast of Vancouver I.; no other data; BCPM98-2, 1(506), taken off west coast of Vancouver I.; no other data; UW-15869, 4(144–400), taken at 48°51.8′N, 124°35.8′W, in Strait of Juan de Fuca, in a trawl; depth not recorded; 27 March 1956; UW-18161, 6(437–512), taken "8 mi out" from Depoe Bay, Oregon at 79 m; method of capture not recorded, 30 August 1964; CAS 19191, 1(403), taken at Holmes Harbor, Puget Sound; no other data; OSU-OTB-180, 1(435), taken at 44°43.5′N, 124°18.1′ W, in a bottom trawl at 96 m, 24 July 1967.

Twelve collections in the California Academy of Sciences, comprising one or two specimens each, and with very incomplete or absent capture data, were taken between Cape Mendocino and San Diego, California (CAS 6832, 7353, 11115, 12751, 12881, 20290, 26491, "Acc. 1954:XI:23," IU 1006, 1069, 1086, 1613 (the IU collections are now at CAS). Similarly, three collections (MCZ 28802, 28803, and 32782), totaling five specimens, with very limited data, were taken in Monterey Bay, California.

Material was taken in 1963 by David Jensen, then of Scripps, in collaboration with the University of Washington Atomic Energy Program. Most specimens were sacrificed to that program. A total of six collections were made between Cape Disappointment, at mouth of Columbia River, off Depoe Bay, Oregon, off Humboldt Bay, and Fort Bragg, California. Numbers of specimens ranged between 6 and 152, and were taken at depths of 38–132 m in bottom traps.

More than 40 collections, comprising nearly 1500 specimens, taken in the southern California area (Pt. Conception to Islas Todos Santos, Baja California, Mexico) were used for certain counts but are not listed among the study material. In addition, hundreds of specimens in the Scripps Marine Vertebrate Collection taken off San Diego were examined for certain characters only and are not listed. However, all collections from outside the Southern California area are listed.

Southernmost collections SIO59-92, 1(345), 28°23′ N, 115°21′W, 280 m; SIO62-91, 3(164–207), 28°11′N, 115°23′W; SIO64-951, 1(363), 31°08′N, 116°35′W, 137 m; SIO71-114, 30(300–465), 28°21′N, 115°43′W, 384 m; SIO71-121, 7(283–384), 28°18′N, 115°29′W, 311–330 m; SIO71-126, 83(195–460), 30°22′N, 116°07′W, 201 m; SIO73-373, 2(320–395), 28°50′N, 114°48′W, 92–95 m.

Distribution Nootka Bay, west side of Vancouver Island, British Columbia, Canada, to Pt. San Pablo, Baja California (about 27°14′N, 114°30′W). Although *E. stoutii* has been reported from southeastern Alaska, we have found no valid records of capture north of Nootka Bay (about 49°33′N, 126°38′W). Despite this extensive range of about 2200 miles, no significant variation in counts or measurements with latitude was demonstrated.

Carl L. Hubbs, at USNM, 28 June 1972 (personal notes), examined collections from southeastern Alaska, labeled as *E. stoutii*, and found them to be either misidentified or with the capture data indicating localities far from Alaska, as follows: USNM 53963, listed as from southeastern Alaska, but with coordinates indicating the vicinity of Monterey, California; USNM 53964, listed as from Alaska, but with coordinates given as 33°08′N, 118°40′W, the vicinity of Santa Barbara, California. Hubbs recorded this specimen as *E. deani* "without question;" USNM 73737, Albatross Station 3077, east of Sitka, Alaska, labeled as *E. stoutii* but referrable to *E. deani*, based on the skin being jet black and eggs to 38 mm length—a length much greater than found in *E. stoutii* (28 mm); in addition, a collection, UW 02738, four, 332–390 mm TL, was recorded simply as "S.E. Alaska; International Fish Commission, 1931."

Depths of capture range between 16 m off the San Onofre Nuclear Power Plant, near San Clemente, southern California, and 633 m at 31°47′N, 116°50′W, south of Ensenada, Baja California, Mexico.

Latitude may be of limited significance in depths of capture (habitat), as the farthest-north least depth is 44 m, off Humboldt Bay, and the farthest south the 16 m capture off the San Onofre Nuclear Power Plant. The species has been taken by scuba divers between 18 and 21 m near La Jolla, California.

Diagnosis Body slender, only slightly deeper than wide. Prebranchial length greater than branchial length. Branchial apertures 12(10–14). Ventral finfold prominent, the distal margin pale. Eyespots small, prominent, the margins well defined. Color a light brown with pale spotting and small blotches common.

Three fused cusps (multicusp) on upper and two fused cusps on lower sets of cusps.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated herein.

Body slender, only slightly deeper than wide, progressively laterally flattened toward tail. Tail spatulate, its ventral profile not slanting downward, but lying on a straight line with ventral profile of body, its depth 43% (30–56%) of its length. A thin, well developed, pale-margined finfold extends from cloaca around tip of tail, ending about over cloaca. Tail length usually greater than branchial length, but is equal-to in 12% and less-than in 8% of 421 specimens. Ventral finfold prominent, with pale distal margin. Head at eye spots about as deep as wide, narrowing toward rostrum. Eyespots small, with distinct margins. Barbels small, usually without pale tips. Second barbel usually longer than first, the first shorter than second in 41%, about equal to in 51%, and longer than second in 7% of 315 specimens. First barbel 51% (41–84%), the second 64% (49–98%) of third barbel. Length of first nasal barbel is given in Table 6 and compared with that of other species treated.

Variation occurs in numbers of GA, left and right sides, with higher numbers predominating on the left, 167 (11%) vs. 56 (4%), N-1554 (Table 8).

Head grooves Grooves present above and below eyespots. Two to four (rarely five) grooves lie above eyespots in lines nearly parallel to the longitudinal axis of the body. Grooves below eyespots are arranged in two groups; 2–5 grooves lie transversely, and from 0–3 lie alongside laterad to and nearly parallel with the longitudinal axis. No grooves cross the dorsal midline.

Color Color ranges between a light to purplish-gray to light brown, with occasional pinkish overtones. Pale spots and blotches (piebaldness) are common. Complete albinism and piebaldness was reported by Jensen (1959:798, figs. 1, 2). Dean (1903:295–296, fig. 1) descriped and figured a specimen with large pale areas on head and anterior ventral surface.

DM short, moderately robust, its length 25% (22–28%) of TL, its width 12% (11–13%) of DM length, its depth 74% (64–77%) of its width. Distance from tip of DM to branching of VA 14% (8–20%) of DM length, and that distance is 42% (25–72%) of VA length. VA length 32% (22–40%) of DM length. Numbers of GP in positions relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species treated here. Afferent duct of last GA, left side, always confluent with PCD.

Eggs The largest egg found measured 28.6 × 7.5 mm, in a female of 435 mm TL. Well developed eggs with anchor filaments are visible but encapsulated. The number of almost fully developed eggs (20 mm or longer) varies from 11 (23 × 7 mm) in a 330-mm TL female to 48 (20 × 6 mm) in one of 515 mm TL. Neither specimen had been opened prior to our examination.

Sex was determinable in a female of 179 mm TL (the eggs tiny) and in a male of 200 mm TL.

The sex ratio of the study material is essentially equal. Of a total of 870 specimens for which sex was reliably determined, 49% were female, 51% male. This ratio contrasts notably with other species described herein, in which females dominated by 60–74%. The maximum size of each sex appears to be equal, the largest male measuring 550 mm TL, the largest female 515 mm TL. Four large females ranged between 491 and 500 mm TL, the next largest 475 mm TL.

Discussion Lockington (1878:792–793) very briefly described *Bdellostoma stoutii* as, "Eleven gill openings on each side; ten teeth in the anterior and nine in the posterior series. 15½″ long. Eel River, Humboldt County."

There is no doubt that the specimen represented a hagfish, but Lockington's subsequent statement indicates that perhaps he confused it with a species of lamprey, possibly *Lampetra tridentata*, as he stated, "It is rather singular that this fish, which is abundant in Eel River and is sold for food, and also occurs in this harbor, should have hitherto escaped notice. I believe it to be the only species of its genus hitherto found on the Pacific coast of North America; and it differs from *Bdellostoma polytrema*, a species which occurs along the coast of Chile, both in the number of its gill openings and that of the teeth, *B. polytrema* having fourteen of the former and twelve of the latter in each series."

There can be no serious question as to the pertinence of the name *stoutii* to this species, although the diagnosis is extremely short and Lockington ascribed the species primarily to Eel River, indicating it as abundant there. But he added, "also occurs in this harbor," meaning, presumably, San Francisco Bay, since there is no harbor at the mouth of Eel River, but only an estuarine embayment.

Perhaps the specimen was sent from near the mouth of Eel River, almost certainly from central or northern California. We maintain the name *stoutii* because it is the only other species of the genus from the area fitting the description. *Eptatretus deani* is a deep purplish-black in color, not light brown. It generally occurs at much greater depths, and it is unlikely that a fisherman would have taken *E. deani* in the 1870s because of this greater depth of habitat. Unfortunately, Lockington did not state the numbers of prebran-

chial pores, which, aside from color, is an important character separating the two species.

Lockington did not designate his specimen as a holotype or state that it was deposited anywhere. If deposited, the most likely place would have been the California Academy of Sciences. W.E. Eschmeyer (Calif. Acad. Sci., San Francisco, pers. commun.) has informed us that Lockington's specimen is not now at the Academy, and stated that it and any record of it may have been destroyed in the San Francisco earthquake and fire.

Therefore, in view of the possible confusion of *E. stoutii* with *E. mcconnaugheyi*, especially off southern California, we designate as neotype of *Eptatretus stoutii*, SIO68-426, a male, 530 mm TL, taken near the whistler buoy at entrance of Humboldt Bay, California. This locality is about 8 miles northerly from the mouth of Eel River, the type locality of Lockington's *Bdellostoma stoutii*.

Discussion

The relationship of the five species treated above superficially appear to be close. We are aware of the speculative and debatable nature of intraspecific variation, and that any proposed new species may be considered a variant of a similar-appearing, sympatric known species.

Thus, it may be argued that *E. deani* and *E. fritzi* are mere variants, due primarily to their very dark coloration, much darker than in any of the other species treated, and due perhaps to their sympatric occurrence in the presently restricted range of *E. fritzi* near Guadalupe Island, Mexico. However, the virtually non-overlapping numbers of prebranchial slime pores, 7(4–10) in *E. deani* vs. 12–13(10–15) in *E. fritzi* (Table 2), alone are adequate for specific separation. In addition, the very large barbels of *E. fritzi* do not occur in *E. deani* (Table 6) of sympatric occurrence or in any portion of the nearly 2600 miles of its total range.

The superficial similarity of *E. stoutii* and the sympatric *E. mcconnaughtyi* also invites speculation as to being mere variants. However, the notable and non-overlapping difference in respective prebranchial lengths alone distinguishes between the two species (Table 1). Also, the numbers of prebranchial slime pores differ significantly, with minor overlap (Table 2).

Similary, *E. stoutii* and *E. sinus* are alike in most counts and proportions, but the very prominent ventral finfold of *E. stoutii* does not occur in *E. sinus*, where it is absent or vestigial. Also, when fresh material of each is compared, the much darker reddish-brown of *E. sinus* contrasts sharply with the much lighter gray-reddish brown of *E. stoutii*.

All the above principal characters differentiating the five species are constant, often non-overlapping, and show little or no variation within species.

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Table 1

Averages and ranges (in thousandths of total length) of selected body proportions for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values for type specimens are given first and followed in parentheses by ranges in values for all material.

Species	Average (range of values)				
	E. mcconnaugheyi	*E. fritzi*	*E. sinus*	*E. deani*	*E. stoutii*
N (Size range in mm)	91 (147–470)	233 (207–592)	458 (129–481)	460 (130–523)	520 (179–468)
Preocular length	62 (45–74)	54 (48–82)	52 (41–82) *	61 (42–89)	53 (40–77)
Prebranchial length	153 (147–181)	198 (176–245)	226 (197–278)	175 (144–204)	240 (187–253)
Branchial length	200 (155–216)	140 (115–158)	113 (92–172)	155 (127–182)	138 (115–142)
Trunk length	532 (482–557)	499 (462–556)	501 (450–540)	517 (480–555)	509 (470–535)
Tail length	130 (122–161)	158 (132–181)	151 (102–174)	151 (126–192)	134 (104–178)
Tail depth	72 (60–88)	65 (58–92)	78 (48–90)	80 (52–103)	55 (45–83)
Body depth with finfold	91 (61–98)	No finfold	67 (49–104)*	78 (47–105)	62 (50–97)
Body depth without finfold	89 (55–90)	63 (53–102)	58 (46–101)*	72 (45–105)	51 (41–90)
Body depth at cloaca	53 (47–71)	56 (45–72)	61 (39–86) *	63 (38–85)	53 (38–79)

*330 specimens measured.

Table 2

Numbers of gill pouches, prebranchial, branchial, and tail slime pores for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values, left side, for type specimens are indicated by an asterisk.

Gill pouches

	9	10	11	12	13	14	*N*	$\bar{X}$	$\hat{\sigma}$
E. mcconnaugheyi				28	67*	2	97	12.73	0.487
E. fritzi		31	261*	64			356	11.09	0.508
E. sinus	77	248*	103	7			435	10.09	0.685
E. deani		21	536	43			600	11.04	0.325
E. stoutii		2	173	691*	63	2	931	11.88	0.507

Prebranchial slime pores

	4	5	6	7	8	9	10	11	12	13	14	15	16	17	*N*	$\bar{X}$	$\hat{\sigma}$
E. mcconnaugheyi			1	5	27	50*	11	2							96	8.74	0.845
E. fritzi							3	40*	123	118	31	3			318	12.45	0.898
E. sinus							3	27	85	142*	117	44	14	3	435	13.26	1.231
E. deani	1	7	90	275	197	23	7								600	7.26	0.854
E. stoutii							2	29	142	366	315*	59	7		920	13.27	0.946

Branchial slime pores

	8	9	10	11	12	13	14	15	16	*N*	$\bar{X}$	$\hat{\sigma}$
E. mcconnaugheyi				15	52	16*	5	2	2	92	12.27	1.012
E. fritzi		14	233	105*	4					556	10.28	0.549
E. sinus	72	246*	107	10						435	9.13	0.698
E. deani		16	425	125	30	4				600	10.30	0.636
E. stoutii		3	151	587	80*	1	1			823	10.91	0.551

Tail slime pores

	7	8	9	10	11	12	13	14	15	*N*	$\bar{X}$	$\hat{\sigma}$
E. mcconnaugheyi		2		21	44*	22	8			97	11.13	0.915
E. fritzi		2		19	87	149	80*	18	1	356	11.96	0.999
E. sinus	2	28	130	168	76*	22	7	2		435	9.90	1.088
E. deani			7	125	224	188	47	5	1	600	11.27	0.958
E. stoutii		4	64	239*	357	125	22	2		813	10.75	0.935

Table 3

Numbers of trunk slime pores for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values, left side, for type specimens are indicated by an asterisk.

	Trunk slime pores																		
	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	*N*	$\bar{X}$	σ
E. mcconnaugheyi																			
Southern California								8	7	6	13	13*	8	3	2		60	46.03	1.871
Gulf of California				1	2	3	4	11	11	3	2						37	43.08	1.566
E. fritzi					2	3	15	38	85	112	67*	24	9	1			356	44.77	1.413
E. sinus	1	4	10	35	64	102	86*	65	40	12	7	7	1	1			435	41.67	1.943
E. deani				1	2	6	38	87	137	152	99	51	22	5			600	44.70	1.601
E. stoutii				1	8	38	96	154	196*	154	110	41	13	5	2	1	819	44.12	1.726

Table 4

Numbers of total slime pores for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values, left side, for type specimens are indicated by an asterisk.

	E. mcconnaugheyi					
Total slime pores	Southern California	Gulf of California	*E. fritzi*	*E. sinus*	*E. deani*	*E. stoutii*
66				1		
67		2		2	2	
68				9	5	
69				11	16	
70		1		16	26	
71		2		39	48	1
72	2	5		57	100	1
73	2	8		53	111	1
74	5	11	1	63	98	11
75	3	3	6	60*	78	26
76	2	1	14	59	63	61
77	11	1	38	21	34	107
78	12	2	50	16	16	142
79	9	1	87	12	2	141
80	6*		71	9	1	116*
81	2		46*	4		100
82	4		23	3		60
83	1		10			29
84	1		8			12
85			2			7
86						3
87						
88						1
N	60	37	356	435	600	819
$\bar{X}$	77.80	73.43	79.36	73.98	75.91	79.03
σ	2.650	2.444	1.909	2.796	2.186	2.280

Table 5

Numbers of anterior and posterior unicusps, and total cusps, for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values, left side, for type specimens are indicated by an asterisk.

Anterior unicusps

	6	7	8	9	10	N	$\bar{X}$	δ
E. mcconnaugheyi		25	151*	15		191	7.95	0.455
E. fritzi		73*	266	32	1	372	7.90	0.531
E. sinus	62	453*	336	21		872	7.36	0.649
E. deani	3	62	604	308	11	988	8.27	0.601
E. stoutii	16	524	390*	11	1	942	7.42	0.555

Posterior unicusps

	6	7	8	9	N	X	δ
E. mcconnaugheyi		40*	143	8	191	7.83	0.472
E. fritzi		37	270*	65	372	8.08	0.518
E. sinus	11	310*	491	60	872	7.69	0.614
E. deani		233	680	75	988	7.84	0.535
E. stoutii	1	347	570*	21	942	7.65	0.531

Total cusps

	34	35	36	37	38	39	40	41	42	43	44	45	46	N	X	δ
E. mcconnaugheyi					1	3	11*	14	48	9	4	2		95	41.60	1.364
E. fritzi					3	5	29*	22	75	25	17	7	3	186	41.92	1.527
E. sinus	1	3	18	13	83*	46	92	39	105	16	15	1	4	436	40.10	2.089
E. deani				1	5	12	55	59	160	68	25	14	3	402	41.86	1.433
E. stoutii			3	4	84	66	126	76	93*	13	5	1	1	471	40.16	1.583

Table 6

Numbers, averages, and ranges of lengths (in mm) of first nasal barbel, left side, for 25-mm increments of total length of five species of hagfishes, genus *Eptatretus*, from the Pacific coast of North America.

	E. mcconnaugheyi	*E. fritzi*	*E. sinus*	*E. deani*	*E. stoutii*
	Average N(Range)				
200-225	3.0 3(2.6-3.5)	6.5 1(-)	2.2 6(1.5-2.6)	3.3 16(2.4-4.5)	2.3 20(2.0-3.0)
226-250	3.3 5(2.9-3.8)	5.9 4(5.6-6.2)	2.6 7(2.0-3.9)	3.5 33(2.6-4.5)	2.8 16(1.9-3.2)
251-275	3.9 8(3.1-4.6)	6.1 3(5.7-6.4)	2.8 25(2.3-3.7)	3.6 31(2.5-4.5)	3.0 52(2.0-4.0)
276-300	4.1 12(3.2-4.9)	6.9 4(6.3-7.2)	2.9 50(2.2-4.3)	4.2 30(3.3-5.3)	3.3 70(2.2-4.5)
301-325	4.2 13(3.6-5.4)	6.3 8(5.0-6.9)	3.1 71(2.0-4.4)	3.8 39(3.2-5.2)	3.5 77(2.4-4.6)
326-350	4.5 10(3.8-5.0)	6.8 24(6.5-9.6)	3.4 80(2.1-4.4)	4.1 42(2.5-5.5)	3.7 110(2.5-5.2)
351-375	4.9 11(4.1-6.3)	7.4 40(5.6-9.1)	3.1 72(2.7-5.6)	4.4 103(2.8-6.0)	3.7 127(2.5-5.1)
376-400	4.9 8(3.9-5.6)	7.8 49(6.2-8.9)	4.0 35(3.0-5.2)	4.6 202(3.0-6.6)	4.1 148(2.6-6.0)
401-425	6.1 6(5.2-7.0)	7.7 71(6.5-10.2)	4.2 17(3.5-5.4)	5.0 235(3.1-6.9)	4.2 109(2.9-5.3)

Table 6 (continued)

	Average *N*(Range)				
	E. mcconnaugheyi	*E. fritzi*	*E. sinus*	*E. deani*	*E. stoutii*
426–450	6.0 6(5.0–7.1)	8.2 50(7.4–10.2)	3.9 8(2.9–5.8)	5.1 174(3.1–7.0)	4.3 65(2.8–6.1)
451–475	6.5 2(6.5–6.5)	9.8 42(7.6–10.8)	3.8 2(3.2–4.4)	5.3 68(3.8–6.6)	5.3 33(3.7–5.9)
476–500	6.8 1(—)	8.9 21(7.2–10.3)	4.1 6(3.8–4.4)	5.4 28(4.0–6.5)	4.7 11(3.9–6.0)
501–525	6.0 2(5.8–6.1)	10.4 9(9.1–11.3)		5.2 10(4.1–5.9)	5.0 13(3.8–6.9)
526–550		10.9 7(10.3–11.7)		4.7 1( )	4.4 8(4.3–5.4)
551–575		10.4 2(9.7–11.3)		4.6 1(—)	6.1 1(—)
576–600		10.2 2(9.5–10.8)			6.8 1(—)
N	87	273	379	1013	861

Table 7

Gill pouches, both sides, in positions relative to Areas I, II, and III of the branchial regions of five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Areas are identified in Figure 4. Values, left side, for type specimens are indicated by an asterisk.

Gill pouches	0	1	2	3	4	5	6	7	8	9	10	*N*	$\bar{X}$	δ
Area I														
E. mcconnaugheyi						2	13	23	45*	34*	9	126	7.98	1.137
E. fritzi				9	49	34*	8					100	4.41	0.763
E. sinus	2	61*	136	103	23	11	5					341	2.40	1.067
E. deani				1	46	62	11					120	4.69	0.643
E. stoutii		7	61	75*	49	19	1					212	3.07	1.023
Area II														
E. mcconnaugheyi	5	13	42*	30*	23	13						126	2.73	1.275
E. fritzi	2	7	12	43*	31	5						100	3.09	1.040
E. sinus	7	20	85	151	65*	11	1					341	2.84	0.994
E. deani	30	44	43	3								120	1.16	0.827
E. stoutii	19	38	68	65*	13	9						212	2.20	1.197
Area III														
E. mcconnaugheyi	4	25*	80	16								126	1.86	0.663
E. fritzi			9	42*	35	13	1					100	3.55	0.865
E. sinus		7	11	13	65	125*	101	17	2			341	4.97	1.229
E. deani				3	16	71	28	2				120	5.08	0.726
E. stoutii				1	3	17*	71	87	32	1		212	6.60	0.933

Table 8

Numbers and percent of occurrence of higher numbers of branchial apertures on left and right sides of five species of hagfishes (genus *Eptatretus*) from the Pacific Coast of North America.

Species	*N*	Higher on left side	Higher on right side
E. mcconnaughey			
Southern California	61	4 (6%)	5 (8%)
Gulf of California	37	5 (19%)	0
E. fritzi	316	81 (26%)	0
E. sinus	446	63 (14%)	7 (2%)
E. deani	1145	125 (11%)	21 (2%)
E. stoutii	1554	167 (11%)	56 (4%)
Totals	3559	445 (12.5%)	89 (2.5%)

Age and Growth of Bluefish *Pomatomus saltatrix* from the Northern Gulf of Mexico and U.S. South Atlantic Coast

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The bluefish *Pomatomus saltatrix* is a migratory coastal pelagic fish generally found in temperate and warm continental shelf waters of all oceans (Briggs 1960). The species occurs along the east coast of the United States and the coast of the Gulf of Mexico. Important commercial and recreational fisheries for bluefish exist throughout the U.S. range (Wilk 1977).

Age and growth studies have been conducted on bluefish from U.S. Atlantic waters (Hamer 1959, Backus 1962, Lassiter 1962, Richards 1976, Wilk 1977), but not from the Gulf of Mexico. The primary purposes of this study were to evaluate and use the best of several bony structures to estimate the age and determine growth of bluefish from the northern Gulf of Mexico (hereafter referred to as Gulf) and from the U.S. Atlantic coast.

Methods

Bluefish from the northern Gulf gillnet fishery were sampled monthly from 1978 through 1982 (Feb–Nov) and in the Atlantic along the southern U.S. east coast in 1980 and 1981 (Jan–July). These samples were augmented by catches from the seine and hook-and-line fisheries. The Gulf samples were collected from the coastal waters off northwest Florida and Louisiana, while Atlantic samples were taken along the coast from South Carolina to Florida.

Fork length (FL) to the nearest millimeter (mm), weight (W) to the nearest gram (g), and sex were recorded from 1190 Gulf and 842 Atlantic bluefish, and one or both otoliths (sagittae) were removed, wiped clean, and stored dry in vials. A subsample of 100 fish representing the entire size range of bluefish caught in the Gulf during May and June 1978 was selected for comparison among ageing structures. From these 100 fish, in addition to otoliths, the tenth vertebra anterior to the hypural plate was removed and scales were taken from the left side under the pectoral fin. Vertebrae were cleaned and air-dried. Both vertebrae and scales were stored dry in envelopes.

Otoliths were placed in glycerol, sulcus acousticus down, in a black dish and were examined under reflected light using a binocular-dissecting microscope with an ocular micrometer. The most legible otolith from each fish was examined for age marks. The second otolith from 25 of the bluefish was sectioned to allow interior examination. The otoliths were embedded in Lakeside 70C thermoplastic cement and, to include the locus, 2 or 3 thin sections (0.15 mm) were cut along the transverse plane, using a Buehler isomet slow-speed saw. The cement was dissolved with isopropyl alcohol, and then the otolith sections were mounted on glass slides and examined on a black background in the manner of whole otoliths.

On whole or sectioned otoliths an opaque zone (mark) preceded by a translucent (hyaline) zone (Fig. 1a) was assumed to be an age mark. Measurements (OR) were made along the longitudinal axis of the rostrum from the focus to the distal edges of the marks and of the otolith. A determination of the edge character (opaque or translucent) was made, and marks were counted. A mark was not considered complete, so not counted or measured, unless the portion of the otolith distal to it was translucent. The rostrum was selected for examination because the postrostrum had an uneven edge which proved difficult to measure.

Vertebrae were stained with crystal violet following the technique of Johnson (1979). To facilitate the observation of age marks, the vertebrae were cut in half, anterior-posteriorly, with a Dremel saw. Both halves of the vertebrae were examined under a binocular-dissecting microscope using reflected light. The most legible posterior centrum was used.

An age mark on the vertebral cone surface was counted if a prominent concentric ridge preceded by a depression was observed (Fig. 1b). Measurements were made from the vertex (focus) of the centrum to the distal edge of each mark as well as to the terminal edge of the vertebra.

Scales were cleaned in a weak solution of water and liquid detergent, then mounted between two glass slides. Scales from 15 bluefish were also impressed on plastic slides with a cold roller press. Both

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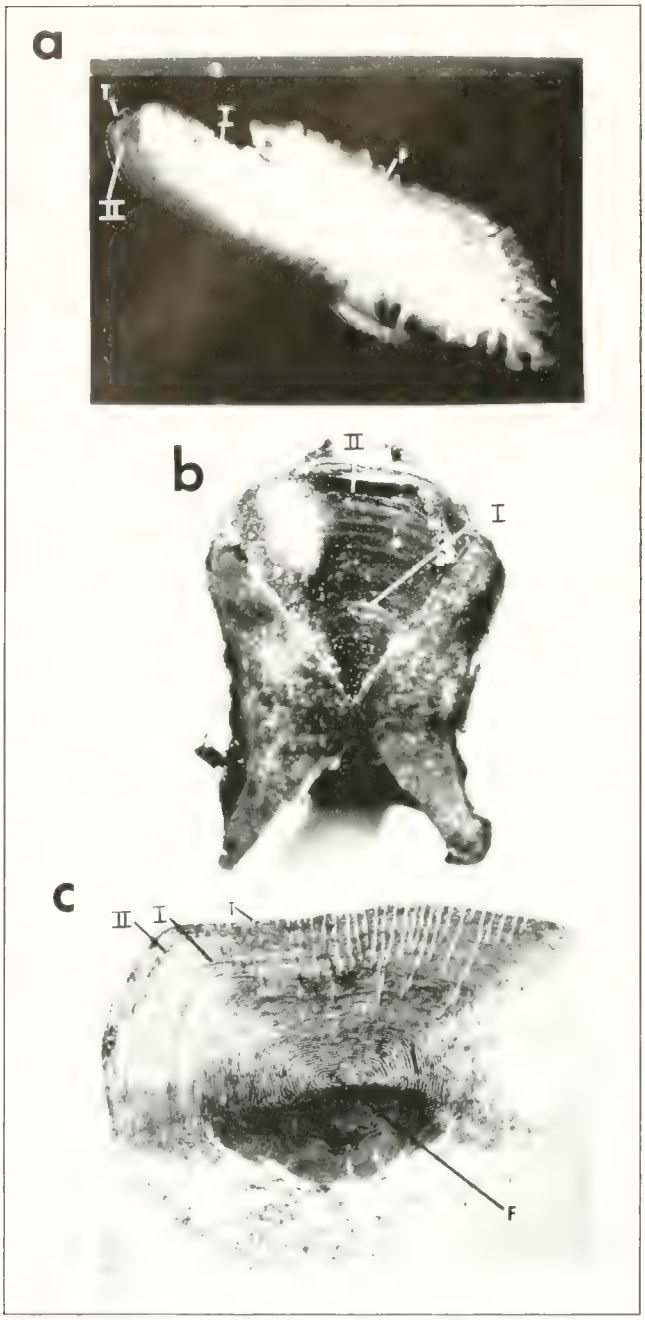

Figure 1

Otolith (a), vertebral section (b), and scale (c) from a 2+ year-old bluefish, 375 mm FL, captured in May. Distal edges of age marks are indicated by Roman numerals. F = focus, T = translucent edge.

slides and impressions were viewed on an Eberbach scale reader. The most legible unregenerated scale was examined for age marks.

On scales and scale impressions an age mark was considered to be a band of widely spaced circuli, usually with broken circuli in the anterior field and/or anastomosis (crossing over) in the lateral field, followed by a series of closely spaced circuli (Fig. 1c). Measurements were made on the projected image from the focus along a radius in the center of the anterior field to the distal edge of the marks and scale edge.

Figure 2

Percent of otoliths with opaque edges by month from Gulf of Mexico bluefish, 1978–82 (*), and U.S. South Atlantic coast, 1981–82 (+).

Two investigators each made one reading of a set of otoliths, vertebrae, and scales from 100 bluefish. All examinations were made without reference to fish length or interpretations of the other investigator.

Computer analyses and plots were accomplished using SAS (Ver. 6.03) software. Backcalculations of length-at-age were accomplished with a program written by the author using means weighted by multiplication of number of samples. Gulf and Atlantic bluefish were analyzed separately. Separate analyses by sex included regressions of fork length and natural log of fork length on otolith length. Least-squares regressions were used to backcalculate length-at-age for males and females separately (Ricker 1975). Multiple regression of sex and age was run to determine difference in length-at-age by sex. Von Bertalanffy theoretical growth curves were calculated using weighted-mean backcalculated fork lengths. The growth equation (von Bertalanffy 1938, 1957) was the following:

$$l_t = l_\infty (1 - e^{-k(t - t_0)})$$

where l_t = length at age,
l_∞ = asymptotic length,
k = growth coefficient, and
t_0 = time when length would theoretically be zero.

Table 1
Backcalculated weighted mean fork lengths of bluefish.

Estimated age group	Number	Mean length at capture (mm)	Mean backcalculated length-at-age (mm) 1	2	3	4	5	6	7	8
From northern Gulf of Mexico, 1978–82										
1	389	364	322							
2	69	441	284	400						
3	30	640	307	415	488					
4	27	719	285	430	515	575				
5	50	745	272	411	510	572	622			
6	29	766	283	424	517	579	628	673		
7	11	766	295	423	512	576	627	668	708	
8	6	767	275	423	530	598	650	695	728	766
Weighted mean			308	413	509	576	627	675	715	766
Annual increment				105	96	67	51	48	40	51
Number			611	222	153	123	96	46	17	6
From U.S. Atlantic coast, 1980–81										
1	389	382	299							
2	161	394	275	362						
3	26	446	265	350	412					
4	12	536	261	342	421	473				
Weighted mean			290	361	415	473				
Annual increment				69	56	58				
Number			588	199	38	12				

Results and discussion

Agreement between investigators in enumeration of marks was highest (92%) with whole otoliths. Lower agreements were attained for scale impressions (67%), vertebrae (33%), and scales (24%). In comparison of whole otoliths with cross-sections taken from the other otolith of a pair, investigators agreed 70% of the time. The close spacing of marks in the sections caused more disagreement in mark enumeration than did the wider spacing in the rostrum of the whole otolith. Also, fractures sometimes occurred in preparation of thin sections, making enumeration of marks on cross-sections of otoliths a less viable option. In addition, 30 otoliths were examined and no difference was found in mark counts on either the rostrum or postrostrum of the otolith or between pairs of otoliths.

To use otoliths, or any structure, for age determination, the deposition of regular detectable age marks is essential. Because samples were obtained from catches of the fishery, no accepted method of direct validation could be employed. However, indirect evidence was established by correlation of the observed mark formation at the distal edge of the rostrum with month. Despite the lack of samples for all months, the results suggested that opaque marks were formed annually in late winter or early spring around March and April in the Gulf and Atlantic samples, respectively (Fig. 2). Gulf bluefish show an unexpected flattening of the curve in June and July. The reason is not known, but a likely hypothesis is a stress-induced check from environmental causes. An alternate hypothesis could be a multiple spawning. However, there are no reports of a summer spawn of bluefish in the Gulf. Backcalculation of length at the time of mark formation is dependent on the relationship between the size of the ageing structure and fish length. Improved fit of the otolith radii (OR) to length relationship occurred when natural log transformation was used for fork length. The equation for Gulf bluefish was $\mathrm{LOG(FL)} = 4.200 + 0.389 \times \mathrm{OR}$ ($r^2 = 0.86$). The equation for Atlantic bluefish was $\mathrm{LOG(FL)} = 4.822 + 0.248 \times \mathrm{OR}$ ($r^2 = 0.61$).

Sexes were pooled for analysis because no significant difference ($\alpha > 0.10$) was found between mean backcalculated fork lengths of sex at age. Studies of Hamer (1959) in the New York Bight, Lassiter (1962) off North Carolina, and Richards (1976) off Long Island also showed no appreciable difference in growth between sexes. The length-weight equation for Gulf bluefish was $\mathrm{W} = -10.02 \times \mathrm{FL}^{2.80}$ and was $\mathrm{W} = -9.18 \times \mathrm{FL}^{2.77}$ for Atlantic bluefish.

Backcalculated lengths-at-age from Gulf and Atlantic bluefish were similar to the respective lengths at

capture (Table 1). The differences were attributed to growth after mark formation. Gulf bluefish were consistently greater in length for age compared with Atlantic bluefish. The difference gradually increased through age-4, the maximum age of the available Atlantic samples.

The Gulf samples included large fish (>600 mm FL) in relatively large numbers (>30% of the sample) only in May and June 1978. During other years, the large fish made up only 4% or less of the Gulf samples. Bluefish of this size are not commonly found in the Gulf. Fable et al. (1981) reported that these fish were decidedly larger than Gulf bluefish observed in 1973 and 1977. Atlantic samples included fish estimated to be no older than age 4 and FL less than 600 mm.

A general comparison with some previous bluefish studies was made (Fig. 3). All other studies used scales to age bluefish and did not report validation. Scale studies were used, as no similar otolith studies could be obtained. Wilk (1977) analyzed scales from bluefish sampled along the Atlantic coast. His results showed slower growth to age-1 than either Gulf or Atlantic samples from this study. By age-2 a larger rate of growth had converged his reported lengths to just short of the Gulf samples from this study, a relationship maintained until age-7 at which point small sample sizes may have contributed to errors. Reported lengths-at-age from scales of Long Island Sound bluefish (Richards 1976) were similar to those of this study. North Carolina spring-spawned bluefish aged by scales (Lassiter 1962) fall within range of Gulf bluefish from this study, but have shorter lengths at each age.

The von Bertalanffy (1938, 1957) theoretical growth parameters derived from this study are:

$$\text{Gulf: } k = 0.180,\ l_\infty = 944,\ t_0 = -1.033$$
$$\text{Atlantic: } k = 0.096,\ l_\infty = 1{,}019,\ t_0 = -2.493.$$

Growth coefficient (k) for Gulf bluefish is within the range of those reported by Lassiter (1962) for North Carolina spring-spawned (0.103) and summer-spawned (0.342) and by Manooch (1979) for Gulf and Atlantic maximum age-8 (0.230) and maximum age-9 (0.340) bluefish. The high growth coefficient of Gulf bluefish reflects the relatively rapid initial growth. The large bluefish taken in the summer of 1978 may influence this coefficient.

Otoliths appear to be better than either scales or vertebrae for ageing Gulf bluefish. Based on the percent of opaque edge occurrence and the close fit with other studies, it appears that age marks on the otoliths of Gulf bluefish are formed annually. Direct validation of age, which was not possible in this study, should be included in future studies. The cause of a higher percent of otoliths with opaque edges in the months of June and July in Gulf bluefish should also be a point of further investigation.

Figure 3

Mean length of bluefish from the Gulf of Mexico and the U.S. Atlantic coast by age in years from this and other published studies. Northern Gulf of Mexico, this study (*); U.S. South Atlantic coast, this study (+); Long Island Sound, NY (Richards 1976), (◇); New York Bight (Hamer 1959), (○); Atlantic coast (Wilk 1977), (□); North Carolina (Lassiter 1962), (△).

Acknowledgments

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Food Habits of Larval Sablefish *Anoplopoma fimbria* from the Bering Sea

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Sablefish *Anoplopoma fimbria* spawn at depths exceeding 400 m (Mason et al. 1983) and their larvae ascend to surface waters soon after hatching (Kendall and Matarese 1987). While in the neuston, they are subjected to highly variable oceanographic conditions. A comparison of the diet of sablefish larvae collected off Oregon and Washington between years that differed markedly in oceanographic conditions (1980 and 1983) revealed a difference in the size of copepods that were ingested (Grover and Olla 1987). Clearly diet can vary between years in one location in response to oceanographic conditions, yet it is unclear how larval diet might vary between distant geographical areas of differing oceanographic conditions.

The aim of the present work was to examine the food habits of larval sablefish that were collected in the Bering Sea in 1979 and compare these findings with those from an earlier study of specimens collected off Oregon and Washington (Grover and Olla 1986, 1987).

Methods

Sablefish larvae were collected during 1979 as part of an ichthyoplankton survey in the Eastern Bering Sea (Walline 1981). Samples were collected using a modified Sameoto neuston sampler, 0.3×0.5 m with 0.505-mm mesh, towed at the surface for 10 minutes at 2–3 knots. Surfacewater temperatures ranged from about 6°C to just over 8°C. Collections were made from the RV *Miller Freeman* between 17 June and 10 July 1979.

All specimens ($N = 127$) from 5 stations (Fig. 1) where larval densities were at least 1/10 m^2 surface area were examined. This represents more than 40% of the total number of sablefish larvae that were collected in 1979.

Larvae were preserved in 10% formalin and were switched into 5% formalin after sorting. Standard length (SL) of each larva was measured, the digestive tract was removed, and contents from the entire digestive tract were identified.

Diet was analyzed in terms of numerical percentage composition (%N), percent frequency of occurrence (%FO), and volumetric percentage composition (%VOL). Prey volumes were calculated from prey dimensions (Grover and Olla 1987). An index of relative importance (IRI = (%N + %VOL) × %FO) (Pinkas et al. 1971) was used for a more comprehensive assessment of prey importance. Data were examined by larval size group (12–15 and 16–23 mm SL).

Prey was categorized as diatoms, copepod eggs, copepod nauplii, *Oithona similis*, *Pseudocalanus* sp. adults and copepodites, *Acartia longiremis*, *Acartia* spp., unidentified copepods, amphipods, and all other prey items.

Prey widths that were used to examine prey-size selection were obtained only from items that were not badly broken or flattened. Over 2900 prey items were measured.

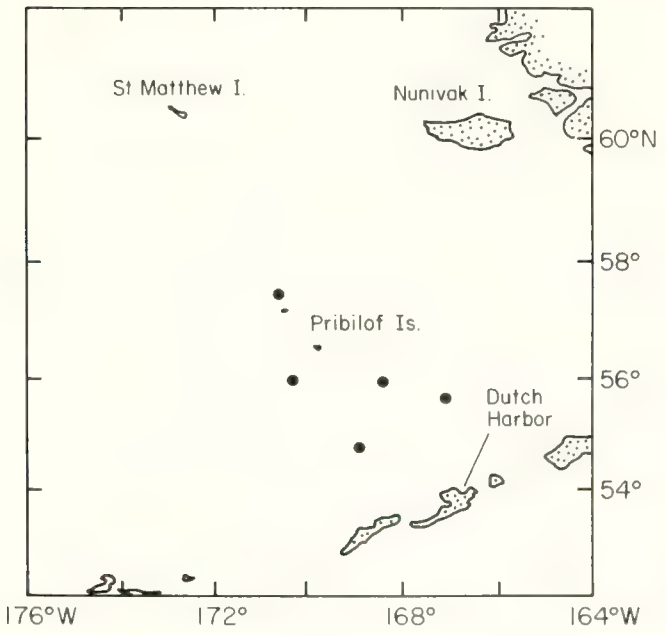

Figure 1
Location of collection stations in the eastern Bering Sea.

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Median widths of diatoms were the smallest (0.01–0.10 mm), followed by copepod eggs, nauplii, and *O. similis* (0.11–0.20 mm), *Pseudocalanus* copepodites, *A. longiremis*, *Acartia* spp., unidentified copepods, and other prey (0.21–0.30 mm), and *Pseudocalanus* sp. adults and amphipods (0.31–0.40 mm).

Results

A single prey-size class was most often ingested by all larvae (Fig. 2A). While both large and small larvae consumed small prey, the ingestion of larger prey by large larvae resulted in the two curves being significantly different ($P<0.01$, Kolmogorov-Smirnov test; Conover 1980). The shared mode of the two curves was attributed to large larvae ingesting a number of small prey items, particularly copepod eggs (0.11–0.20 mm) (Table 1). When we eliminated copepod eggs from the analyses, assuming that they were taken incidentally in the course of ingesting adult female *Pseudocalanus* sp., the prey-size distribution of small larvae did not change noticeably (Fig. 2B). But the removal of copepod eggs from the diet of large larvae shifted the prey-size mode towards larger prey.

Copepod nauplii were the primary prey of small larvae (Table 1). *Pseudocalanus* sp. also comprised a major portion of the diet, with adults and copepodites nearly equal in importance. Unidentified copepods made a small contribution, while *Acartia* spp., *Oithona similis*, and copepod eggs were rather insignificant in the diet of small larvae.

Copepods were the primary prey of large larvae (Table 1), with *Pseudocalanus* sp. adults predominant over copepodites and all other species. A large number of copepod eggs were ingested, while amphipods, unidentified copepods, *Acartia longiremis*, and copepod nauplii made progressively smaller contributions to the diet. The relatively large size of amphipods likely contributed to their being ingested only by large larvae.

The mean number of prey items ingested by small larvae was 26.9, compared with 34.1 by large larvae. The incidence of feeding was 100%.

Discussion

The pattern of prey-size selection observed in the Bering Sea contrasts with the pattern seen for larvae collected off the Oregon and Washington coasts in 1980 (Grover and Olla 1986). In each study functional breaks in diet (e.g., the shift away from dependence on copepod nauplii) were used to define larval size groups. The Oregon–Washington collections were categorized into three size groups: 8.2–12.5, 12.6–20.5, and 20.6–28.5 mm SL. Each size group favored a different peak prey size, with the smallest larvae ingesting the smallest prey, and the largest larvae ingesting the largest prey (Grover and Olla 1986). However, peak prey sizes for the two size groups from the Bering Sea were the same as long as copepod eggs were included in the analyses. Their removal shifted the prey-size utilization curve of large larvae in the Bering Sea towards larger prey.

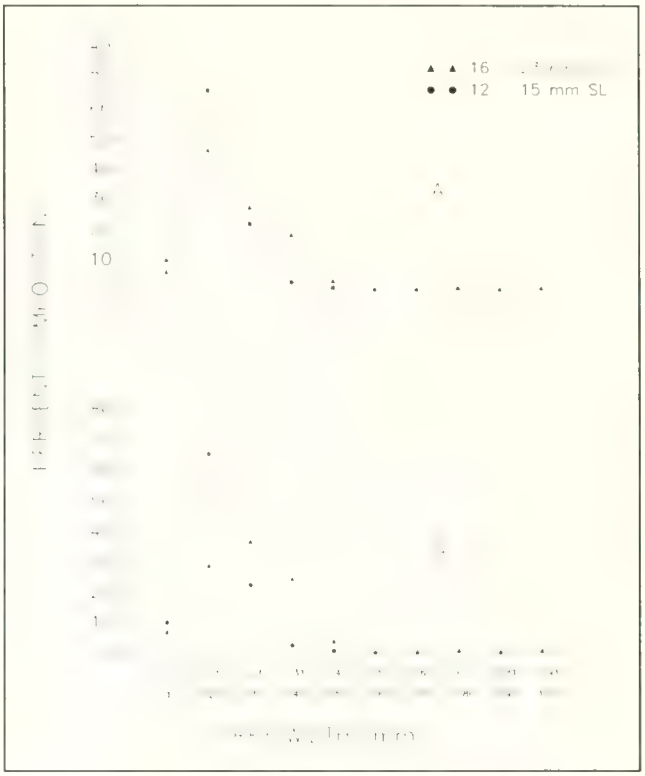

Figure 2
Size of prey selected by two size classes of larval sablefish (12–15 and 16–23 mm SL) in the Bering Sea in 1979: (A) including copepod eggs, (B) omitting copepod eggs.

Copepod eggs had a greater impact on the diet in the Bering Sea than off Oregon due to a difference in the biology of the dominant copepod species ingested in the two regions. The dominant copepod in the diet of large larvae collected off Oregon in 1980 was *Paracalanus parvus* (Grover and Olla 1987), a species that broadcasts its eggs into the sea (Checkley 1980). *Pseudocalanus* sp., the dominant copepod in the diet of larvae collected from the Bering Sea, carries its eggs (Corkett and McLaren 1978) which could thus be ingested incidental to the adults. Nevertheless, as female copepods with eggs were not observed in sablefish guts, and as other copepods that broadcast their eggs (such as all *Acartia* spp.) contributed to the diet, it remains a possibility that some eggs were ingested independently

Table 1

Composition of the diet of larval sablefish in the Bering Sea in terms of the Index of Relative Importance (IRI) and its components: Numerical percent composition (%*N*), frequency of occurrence (%FO), and volumetric percent composition (%VOL), by size class.

	Larval size class							
	12–15 mm				16–23 mm			
Prey	%*N*	%VOL	%FO	%IRI	%*N*	%VOL	%FO	%IRI
Diatoms	0.2	<0.1	4.5	<0.1	3.3	<0.1	30.8	0.8
Copepod eggs	2.6	0.3	22.7	0.4	20.2	0.8	74.4	11.2
Copepod nauplii	74.1	41.6	100.0	77.9	12.9	3.0	43.6	5.0
Oithona similis	2.4	2.5	27.3	0.9	5.0	2.2	38.5	2.0
Pseudocalanus sp. adults	4.2	23.6	39.8	7.4	23.7	55.7	92.3	52.7
Pseudocalanus copepodites	9.6	17.8	50.0	9.2	9.4	8.2	74.4	9.4
Acartia longiremis	0.3	0.8	1.1	<0.1	8.4	8.6	41.0	5.0
Acartia sp.	2.4	4.7	19.3	0.9	2.1	1.7	38.5	1.1
Unident. copepods	3.7	7.4	40.9	3.1	7.5	6.3	56.4	5.6
Amphipods					7.2	13.2	48.7	7.1
Other	0.5	1.2	10.2	0.1	0.3	0.3	7.7	<0.1

of females. However, since the number of copepod eggs in the diet appeared to be positively correlated with the number of adult *Pseudocalanus* sp. ingested, we conclude that most copepod eggs were probably attached to adult female *Pseudocalanus* sp. when they were ingested. The mechanical action of ingestion most likely liberated the eggs from their delicate egg sacs (see Grover 1990). These data suggest that copepod eggs may be important in the diets of larval sablefish and other species in the Bering Sea.

In contrast to the larval diet off Oregon and Washington, copepods >2 mm were inconsequential in the diet of larvae in the Bering Sea. While copepod species with southern affinities were absent from the diet of sablefish larvae collected in the Bering Sea, species with northern affinities, i.e., *Pseudocalanus* sp. and *A. longiremis*, occurred more frequently in the diet of larvae collected in the Bering Sea than off Oregon (Grover and Olla 1987). Euphausiid larvae, appendicularians, and pteropods were absent from the diet of sablefish larvae collected in the Bering Sea, while they made a noticeable contribution to the diet of sablefish larvae collected off Oregon.

Specific differences in prey items could be expected when comparing geographically separated populations; however underlying principles of prey-size selection are assumed to be universal in nature (Hunter 1981). We looked beyond the initial data plots and found a biological explanation as to why the size of prey consumed by large larvae in the Bering Sea differed from the pattern observed off Oregon (Grover and Olla 1986). Our data revealed that copepod eggs have such a confounding influence on prey-size distributions that the mode of their ingestion (i.e., free-floating vs. attached to adults) must be recognized in order to adequately interpret prey-size selection patterns.

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Movement of Tagged Lingcod *Ophiodon elongatus* at Neah Bay, Washington

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Lingcod *Ophiodon elongatus* is an important component of Washington's coastal commercial and sport fisheries (Jagielo 1989). Female lingcod comprise most of the offshore commercial landings, grow faster than males, and attain a larger size. Males predominate in the nearshore sport catch, are typically smaller than females, and perform a nest guarding role during reproduction. These characteristics of the coastal lingcod population suggest the need for an integrated stock assessment which addresses males and females separately and takes the geographic distribution and migratory behavior into account.

This paper reports the movement of lingcod tagged nearshore in the western Strait of Juan de Fuca near Neah Bay, Washington, during 1986–89. Results are presented for tags recovered through 1989 and analyzed by sex and size for extent and direction of movement. I also evaluated tag retention of a wire spaghetti tag applied on the preopercular plate as an alternative to strap, anchor, or dart tags used previously for lingcod tagging (Chatwin 1958, Forrester 1973, Cass et al. 1983, Mathews and LaRiviere 1987).

Methods

From 1986 to 1989, 3478 lingcod were tagged using a chartered commercial vessel trolling with 6–10 jigs from a hydraulic gurdy. Each year fishing occurred from mid-March to mid-April in advance of the sportfishery opening on 15 April. Only fish not injured by capture were tagged and released. All tagged fish were measured to the nearest millimeter, and sex was determined by noting the presence of anal papillae in males.

The tagging area was within 3 miles of the shoreline in the vicinity of Neah Bay, Washington, and extended from the Sekiu River to Makah Bay (Fig. 1). In 1986, the tagging effort was distributed evenly among areas NB-1, NB-2, and NB-3. Area NB-4 was added in 1987, and effort was distributed evenly among the four areas from 1987 to 1989. Most of the tagging occurred at depths between 15–25 m.

In 1986 two tag types were released: 481 fish were tagged with a large dart tag (Floy FT-1) applied dorsally, and 487 fish were tagged with a wire spaghetti tag (Floy FT-4) twist-tied to the preopercular plate. Fish were alternately tagged with one of the two tag types and were released back into the population. Recaptures from 1986 to 1989 for the two tag types are shown in Table 1. In 1987 and 1988, 207 fish were double-tagged with the spaghetti tag to evaluate tag shedding. Through September of 1989, 20 of the double-tagged fish were recovered, all with both tags in place. Since tag shedding appeared to be negligible for the spaghetti tag, only fish released with the spaghetti tag (2997 lingcod) were analyzed for movement trends in this paper.

Recapture information, including the date and location of capture, was obtained both by direct interviews with fishermen and by voluntary returns submitted by fishermen. A $10 reward was paid for the return of tags, which was available directly on landing at Neah Bay.

Migratory and nonmigratory lingcod were defined as fish recaptured at distances greater than or less than 8.1 km (5 miles) from the tagging location, respectively. This reference distance was selected to enable comparisons with previous tagging studies. Chi-square contingency-table analysis was used for comparing release length-frequency distributions of migratory and nonmigratory recoveries and migrational tendency by sex. A chi-square goodness-of-fit test was used to test the null hypothesis that the release length distribution of recaptured lingcod was the same as the release length distribution of all tagged lingcod. Length-frequency distributions were grouped into 5-cm intervals and pooled at the tails so that no expected cell frequency was <1.0 and no more than 20% of the expected cell frequencies was <5.0 (Zar 1974, p. 50). One-way analysis of variance was used to test the null hypothesis that the mean time at liberty was the same for fish that had migrated different distances.

Results

Through September 1989, 393 (13.1%) tagged lingcod were recaptured (Table 2). The percent recaptured for each release group ranged from 9.96% in 1989 to 18.89% in 1986. The lower recovery rate for the 1989 release is probably a reflection of fewer recovery years as compared with releases from 1986 to 1988.

The length distribution of tagged lingcod by sex are shown in Figure 2a. Of all tagged lingcod, 99% were sexed; 84% of this sample were

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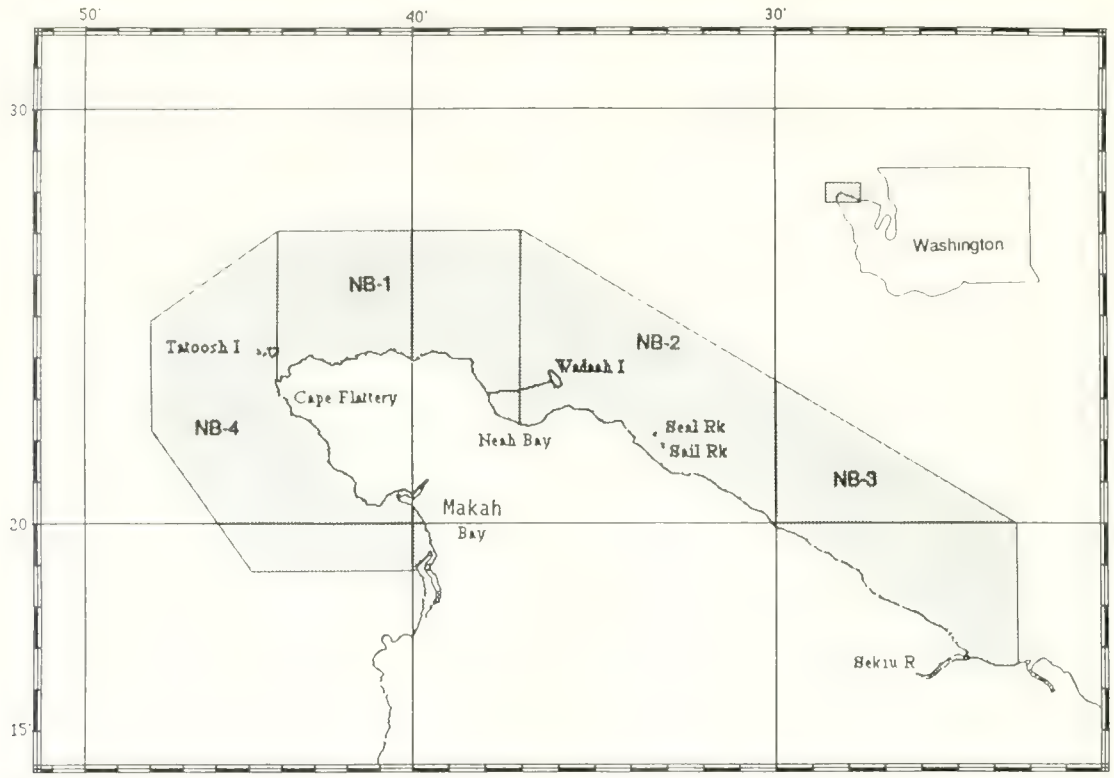

Figure 1
Lingcod tagging area at Neah Bay, Washington.

Table 1
Rates of recapture of tagged lingcod for two types of tags released in 1986.

Tag type	No. tagged	No. tags returned by fishermen 1986	1987	1988	1989	Total	% returned
Large dart (Floy FT-1)	481	41	25	7	1	74	15.38
Spaghetti (Floy FT-4)	487	47	29	13	3	92	18.89

Table 2
Number of lingcod tagged, 1986-89, and recaptured through 1989 by year of recapture.

Year tagged	No. tagged	1986	1987	1988	1989	Total	% recaptured
1986	487	47	29	13	3	92	18.89
1987	564	0	36	20	15	71	12.59
1988	982	0	0	79	55	134	13.64
1989	964	0	0	0	96	96	9.96
Total	2997	47	65	112	169	393	13.11

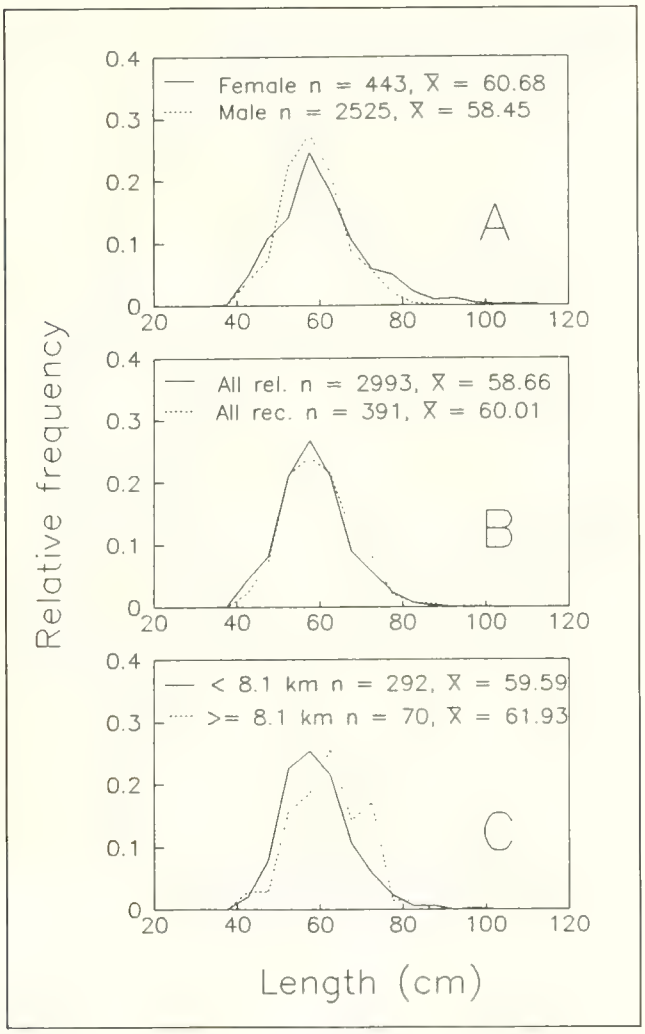

Figure 2

Length-frequency distributions of tagged lingcod. (A) Known male and female lingcod tagged; (B) release length distribution of all lingcod released and all lingcod recovered; (C) release length distribution of all lingcod recovered <8.1 km from release location and all lingcod recovered ≥8.1 km from release location.

males. The average size of tagged males (58.45 cm) was less than the average size of females (60.68 cm). Based on the length-at-maturity values of 46 cm for males and 76 cm for females (Mathews and LaRiviere 1987), approximately 95% of the tagged males were mature, and approximately 10% of the tagged females were mature at the time of tagging.

The average size of all tagged fish recaptured (60.01 cm) was greater than the average size of all tagged fish released (58.66 cm) (Fig. 2b). The null hypothesis that the length distribution of all recaptured lingcod is the same as that of all tagged lingcod was rejected (χ^2 = 14.91 with 7 df; P = 0.0371).

The average size of fish considered migratory (61.93 cm) was greater than those considered nonmigratory (59.59 cm) (Fig. 2c). The null hypothesis that migratory fish had the same length distribution as nonmigratory fish was rejected (χ^2 = 51.42 with 5 df; P<0.00001).

Of the 363 lingcod with known tagging and recapture locations, 70 (19.3%) were recaptured >8.1 km (5 miles) from the tagging location and were considered migratory, while the remaining 293 were recaptured within 8.1 km of the tagging location and were considered nonmigratory (Table 3). Of those that migrated, 46 were recaptured from 8.1 to 50 km from the tagging site, and 24 were recaptured >50 km from the tagging site.

Relative to the tagging location, most of the migratory recaptures were westward and out of the Strait of Juan de Fuca as opposed to eastward and inside the Strait. Of the 70 lingcod judged to be migratory, 54 were recaptured west and north/south of the tagging location, while only 16 were recaptured east and north/south of the tagging location (Table 3). The null hypothesis that male and female tagged lingcod were as likely to be recaptured east and north/south as opposed to west and north/south) of the tagging location was rejected (χ^2 = 20.62 with 1 df; P<0.00001). Recaptures came from as far north as Queen Charlotte Sound (241 miles), as far south as Cape Falcon (149 miles), and as far east in the Strait of Juan de Fuca as Crescent Bay (36 miles). Most of the migratory fish (25) were recovered on trawl grounds off the Washington coast and included those in the vicinity of Cape Flattery (5), the Cape Flattery Spit (9), Umitilla/La Push (4), Destruction Island (4), and Cape Elizabeth (3).

Table 3

Distribution of recoveries of tagged lingcod by distance and direction of migration.

		8.1–50 km			>50 km			Recaptured	
No. tagged	<8.1 km	East	West	Total	East	West	Total	No.	%
2997	293	15	31	46	1	23	24	393*	13.11

*Includes 30 recaptures with unknown recapture location.

Table 4
Distribution of recaptured lingcod by sex and distance of migration.

Sex	Total released	Number recaptured <8.1 km	8.1–50 km	>50 km	Unknown distance	Recaptured Total	%
Male	2526	245	42	24	23	334	13.22
Female	443	47	4	0	6	57	12.87
Unknown	28	1	0	0	1		
Total	2997	293	46	24	30	393	13.11

Thirteen were recovered on Canadian trawl grounds including La Perouse Bank (8) and Swiftsure Bank (4). Twenty of the migratory recaptures occurred within the tagging area between Makah Bay and the Sekiu River (Fig. 1), and 12 recaptures were made east of the study area in the Strait of Juan de Fuca.

Of fish with known sex and recapture location, a higher proportion of male lingcod were migratory as compared with female lingcod. Of 311 male recaptures, 66 (21.2 %) were judged to be migratory, while 4 of 51 female recaptures (7.8%) were considered migratory (Table 4). The null hypothesis that male and female recaptures were equally likely to be migratory was rejected ($\chi^2 = 4.20$ with 1 df; $P = 0.0402$ with Yates correction).

The time span between tagging and recapture for all recaptured lingcod averaged 237.6 days and ranged from 6 to 1197 days (Table 5). The null hypothesis that the average time span between tagging and recapture was the same for fish recaptured at different distances was not rejected ($F_{2360} = 1.50$; $P = 0.2240$).

Table 5
Time span between date of tagging and date of recapture of tagged lingcod with known date of recapture.

Distance between release and recapture	No. recaptured	Time span (days) Mean	Range
<8.1 km	293	224.91	18–1197
8.1–50 km	46	251.85	36–1122
>50 km	24	306.63	78–770
Total	393*	237.61	6–1197

* Includes 30 fish with unknown distance traveled.

Discussion

This study gives qualitative evidence that a portion of the nearshore lingcod population in the vicinity of Neah Bay is vulnerable to the offshore trawl fishery; however, fishery tag recapture data, unadjusted for differential fishing effort, are inadequate to make quantitative statements about the net mixing rates of fish between areas. Clearly, from a harvest management perspective, it is important to know whether offshore stocks of lingcod contribute to nearshore recruitment, or vice versa, since valued fisheries operate in both areas.

Previous studies in the Strait of Juan de Fuca and Strait of Georgia have reported variable lingcod movement and indicate some exchange between inside and outside waters. Hart (1943) observed that fish tagged in the vicinity of the Strait of Juan de Fuca and Seymour Narrows made more extensive migrations than fish tagged in other adjacent inside waters. Of 1993 fish released during 1939–43, 209 were recovered of which 34 (16%) traveled distances >8.1 km (5 miles). For 342 recoveries from tags released in the Strait of Georgia during 1943–54, 73 (21.3%) were recaptured within 1.6 km (1 mile) and 32 (9.3%) were recaptured >8.1 km from the point of release. Of those recaptured >8.1 km, the average time at liberty was 3 years and the net movement was northwesterly within the Strait (Chatwin 1956). Mathews and LaRiviere (1987) reported that of 1692 lingcod tagged during 1976–81 in the eastern Strait of Juan de Fuca and in the vicinity of the San Juan Islands, 74 (49.6%) of 149 fish recovered moved >8.1 km and were judged to be migratory. Most recaptures were south or west of the tagging site; the predominant pattern of movement was south and west through the Strait of Juan de Fuca. Fish tagged in the eastern Strait of Juan de Fuca migrated more than fish tagged in the San Juan Islands. Five recaptures were reported from the Pacific Ocean. The longest movement to the northeast was to Porlier Pass, British Columbia; the longest movement to the southwest was off Newport, Oregon.

Previous offshore tagging studies have reported some movement between the various offshore fishing banks. Reeves (1966) reported that of 437 tagged on La Perouse (Forty Mile) Bank in June of 1960, 284

were recovered of which 74% were captured in the area of release, 21% had uncertain recovery location, and 5% were recaptured away from Forty Mile Bank (as far as Cape Flattery to the south and Ucluelet-Barkley Sound to the north.) The majority of all recaptures (82%) occurred within a 6-week period following the release because of an intensive trawl fishery for lingcod in the vicinity of tagging on Forty Mile Bank. Forrester (1973) reported the release of 2000 tagged lingcod on the Lennard Island trawling grounds in September of 1964; 535 were recovered with known locations of which 92 (17.2%) moved from the tagging site. Most of the fish recovered away from the tagging site were recaptured on Big Bank (southern La Perouse Bank) to the south. Fish were recaptured from as far as Cape Russell to the north and as far as Cape Flattery to the south. Most recaptures occurred in the summer months of the year following tagging (A.J. Cass, Pac. Biol. Stn., Dep. Fish. Oceans, Nanaimo, BC, Canada, pers. commun.). Jack Robinson (Oreg. Dep. Fish. Wildl., Newport, OR, pers. commun.) reported the tagging of 3800 lingcod in offshore waters near Newport, Oregon in July of 1978. Within 17 months, approximately 10% of the tagged fish were recovered of which approximately 9% were recovered away from the area of tagging. Mathews and LaRiviere (1987) reported the results of H. Horton from 522 lingcod tagged off Depot Bay on the central Oregon coast during June 1978–January 1982. Of 19 recaptures reported through 1985, 10 had not moved significantly and 9 (47%) had migrated more than 10 km. Of those that migrated, 2 went a distance of more than 100 km.

Chatwin (1956) reported evidence of homing behavior in Strait of Georgia lingcod. Of 14 lingcod captured at Entrance Island and transported 9.7 km (6 miles) to Departure Bay (Hart 1943), 4 were subsequently recaptured at Entrance Island, and one at Newcastle Island (between Entrance Island and Departure Bay) within 2 years of release. Buckley et al. (1984) reported evidence of homing behavior in Strait of Juan de Fuca lingcod. Of 187 adult lingcod transferred from the eastern Strait of Juan de Fuca to Pulali Point in Hood Canal in 1978, 9 recoveries all were recaptured at distances >8.1 km from the release site. Of the 9, 7 were recaptured northward in the direction of their original capture site.

My results at Neah Bay show more lingcod migratory behavior than most of the previous studies, but less than that reported in the eastern Strait of Juan de Fuca (Mathews and LaRiviere 1987). I found 70 of 363 recaptures (19%) to be migratory. Of the 70 that migrated, 24 (34%) moved in excess of 50 km. Mathews and LaRiviere (1987) reported 74 of 149 recaptures (50%) to be migratory, of which 13 (18%) moved over 50 km. The difference in percent migratory could be due to differences in exploitation rates. The Neah Bay tagging was conducted in March and April, and most tags were recaptured in the spring and summer months immediately following tagging. Most of the tags came from the intense sportfishery operating in the vicinity of Neah Bay, which may have removed potential migrants. Most of those that moved over 50 km escaped the sportfisheries and were recaptured on trawl grounds offshore. In the eastern Strait of Juan de Fuca, tagging was conducted through May and most of the recaptures occurred the year following tagging by Canadian trawlers on Constance Bank (Mathews and LaRiviere 1987). These fish were probably not subject to the same recreational fishing pressure in the vicinity of tagging, and have had a greater opportunity to migrate. The difference in the relative proportion of fish moving >50 km could be due to the distances from release sites to trawling sites; Constance bank is 18 km west of Middle Bank, where much of the eastern Juan de Fuca tagging occurred, while most of the coastal trawling occurs over 50 km from the Neah Bay study area.

The predominance of male fish tagged at Neah Bay can be explained by the different bathymetric distribution of the two sexes. Others have reported that lingcod are distributed by depth according to sex and size; larger fish (mainly females) inhabit deep banks or reefs, while smaller fish (typically males) inhabit the shallower reefs nearshore (Chatwin 1956, Forrester 1973, Miller and Geibel 1973, Cass et al. 1984). Mathews and LaRiviere (1987) noted a similarly skewed sex ratio for fish tagged nearshore in the eastern Strait of Juan de Fuca.

While the results of this and previous nearshore tagging studies give evidence of nearshore to offshore movement, a coherent pattern is not evident and a reliable working model of coastal lingcod migration is not yet available. Migratory recaptures from the present study were typically larger at the time of release than nonmigratory fish, suggesting a size threshold for movement; however, Mathews and LaRiviere (1987) failed to show a relationship between size at release and migratory tendency, and Hart (1943) concluded that large lingcod move less than small lingcod and that "some but not more than 5% of lingcod are more or less migratory during each year." Since the tagging at Neah Bay occurred nearshore in a narrow depth range (15–25 m) where the relative abundance of females is low, the effect of sex and size on lingcod movement reported here is likely biased with reference to the population as a whole. This depth-related bias may explain the discrepancies between this and other studies with regard to lingcod movement.

Some level of female movement from offshore to nearshore areas for spawning is implied by the high

relative abundance of females at depth, though the nature and extent of such spawning migrations is poorly understood. It is unclear, for instance, whether females spawning nearshore reside nearby at depth and make vertical seasonal migrations to spawn, or whether female lingcod migrate seasonally from the deep offshore trawling grounds to spawn nearshore. Such movements have been widely accepted as fact, though tagging experiments to date have failed to confirm a seasonal mass spawning migration (Miller and Geibel 1973).

An appropriate tagging study design to model coastal lingcod movement will require tagging in both nearshore and offshore areas and the estimation of both the probability of survival as well as the probability of capture across the time-area strata. To separate movement from survival, a minimum of three samples is needed. Iwao (1963) and Arnason (1972) gave models under this scenario, but only for the case with multiple recaptures. These approaches are not applicable to most fisheries tagging studies in which individuals are recaptured once by a commercial or recreational fishery and recovered dead. Potentially more applicable to fisheries tagging studies, Schwarz (1988) and Schwarz and Arnason (1990) have extended the traditional exploitation-based models of Brownie et al. (1985) to include tag recoveries over both time and space, and Hilborn (1990) recently provided a general framework for analysis of movement and mortality which incorporates a population dynamics and movement model using a maximum-likelihood minimization approach.

In conclusion, this study gives evidence that a component of the lingcod population at Neah Bay is exposed to fishing mortality from the offshore trawling fleet. Research is needed to yield quantitative estimates of lingcod mixing rates, stratified by sex and size, between the nearshore and offshore fishing grounds. These mixing rates will be essential to establish mortality rates by sex and age for the population as a whole, to clarify the collective impact of the nearshore and offshore fisheries on the coastal lingcod population.

Acknowledgments

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Captive Tunas in a Tropical Marine Research Laboratory: Growth of Late-larval and Early-juvenile Black Skipjack *Euthynnus lineatus*

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Little is known about the biology of tunas during larval and early-juvenile stages because they are relatively inaccessible to scientists. In the eastern Pacific Ocean fishermen seldom catch juveniles of less than about 30 cm in length. Concurrent laboratory and field studies of tuna growth and mortality are important to gain insight into the recruitment process. These considerations motivated the Inter-American Tropical Tuna Commission (IATTC) to establish a research center at Achotines Bay in the Republic of Panama, a site located near tuna spawning grounds (Fig. 1).

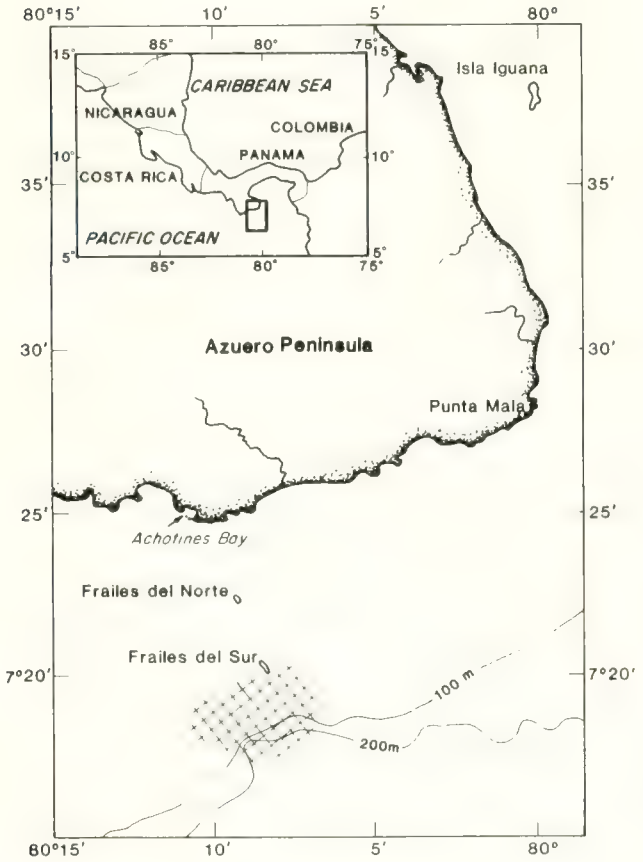

Figure 1
Location of the study site (cross-hatched) south of Achotines Bay, Panama. The IATTC's Achotines Laboratory is situated on the east side of the Bay.

Black skipjack tuna *Euthynnus lineatus* are not commercially important; however, their similarity to other tunas makes them valuable subjects of study. Their distribution is limited to tropical and subtropical regions of the eastern Pacific Ocean (Collette and Nauen 1983), with two stray specimens reported from the Hawaiian Islands (Matsumoto 1976). For many years, *E. lineatus* was thought to inhabit only coastal waters and waters around islands (Calkins and Klawe 1963, Yoshida 1979). However, recent fishing records show that black skipjack also occur in oceanic habitat (Schaefer 1987, fig. 1; Bayliff 1988a, fig. 62).

Clemens (1956) reported the only previous information on rearing and growth rates of early-juvenile black skipjack. Some information was reported by Peterson (1983:54) on the growth of 32–51 cm fork length (FL) black skipjack in the field, based on tagging studies and length-frequency modal progression analysis. Houde and Richards (1969) described the growth of larval little tunny *E. alletteratus* reared in the laboratory from planktonic eggs. The larvae were fed unspecified quantities of mostly copepod nauplii and copepodites, and grew from less than 3.0 mm total length at hatching to almost 8.5 mm in 18 days, a rate of about 0.3 mm/day. No data are available on larval growth of kawakawa *E. affinis* (Yoshida 1979).

The purpose of this note is to report the establishment of the Achotines Laboratory in Panama, to describe sampling results and rearing procedures of late-larval and early-juvenile black skipjack tuna, and to report growth experiments on captive black skipjack.

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Laboratory studies of growth are important in light of evidence in other fishes that variability in growth rates in the wild can affect early-life-stage duration, potentially resulting in large changes in larval survival and subsequent recruitment (Houde 1987).

The Achotines Laboratory and study area

The IATTC's Achotines Laboratory is located on a broad south-facing headland on the southern tip of the Azuero Peninsula in the Los Santos Province of the Republic of Panama (Fig. 1). This site is located at the northwestern part of the Panama Bight, which extends from Panama to Ecuador (Forsbergh 1969). The Panama Bight is a region with large seasonal variations in atmospheric and oceanic characteristics, in part influenced by the seasonal position of the intertropical convergence zone (ITCZ). Sea-surface temperature data (Fig. 2) clearly show an upwelling cycle driven by the Caribbean trade winds when the ITCZ is displaced to the south, typically beginning in December and lasting at least through April. The continental shelf is narrow, 2–30 km in width, off the Azuero Peninsula, but widens abruptly on either side of the Peninsula. Thus, oceanic habitat, thought to be a requirement for tuna spawning, occurs close to shore. Scombrid larvae and early juveniles are routinely captured as close as 9 km from Achotines Bay. The following late-larval and early-juvenile scombrids have been captured and held in the laboratory with varying degrees of success: black skipjack tuna, yellowfin and/or bigeye tuna (*Thunnus albacares* and/or *T. obesus*)[1], frigate and/or bullet tuna (*Auxis thazard* and/or *A. rochei*)[2], sierra *Scomberomorus sierra*, chub mackerel *Scomber japonicus*, and Indo-Pacific bonito *Sarda orientalis*.

Materials and methods

Larval and early-juvenile fishes were attracted to a bright underwater light at night (nightlighting) in the vicinity of the 100- and 200-m isobaths (Fig. 1) during October 1986–April 1988. A 24-volt DC 300-watt light was lowered from a drifting boat to a depth of about 14 m, left for about 5 minutes, and slowly raised to a depth of 1–2 m. Late-larval and early-juvenile[3] black skipjack tuna approaching the light were collected by dipnet and quickly placed into 61 × 76 cm polyethylene bags with rounded corners containing aerated seawater. A water conditioner, Fritz-guard, was added to the water to minimize damage to the fish from mucous loss caused by abrasion. Time from capture to arrival at the laboratory ranged between 1 and 3 hours. Sea-surface temperature, weather, and sea conditions were recorded. The fish which did not survive nightlighting and transfer procedures were measured (standard length, SL, to nearest 0.1 mm) and weighed (round wet weight to nearest 0.001 g) soon after capture.

At the laboratory, the captive fish were placed in 1.2-m diameter circular fiberglass tanks containing 0.3 m^3 of aerated seawater with a weak current. Water

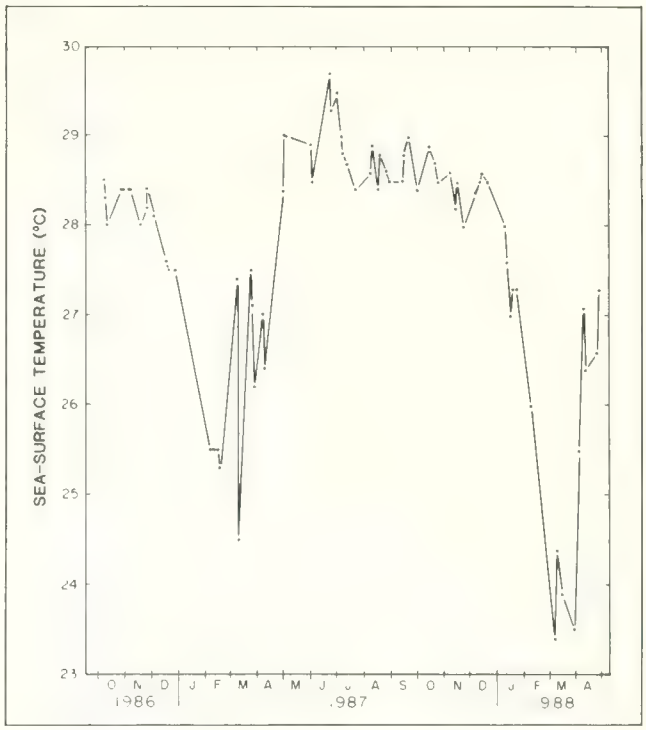

Figure 2
Sea-surface temperatures taken while nightlighting in the sampling areas (Fig. 1) off the Achotines Laboratory.

[1]Early-juvenile *T. albacares* and *T. obesus* cannot be distinguished on the basis of meristic, morphological, pigmentation (Matsumoto et al. 1972), or osteological characters (Potthoff 1974). However, an electrophoretic distinction between yellowfin and bigeye adults provides a means of separating the larvae and early juveniles (Graves et al. 1988).

[2]Larval and early-juvenile *Auxis thazard* and *A. rochei* have been distinguished by minor differences in pigmentation and body depth, but identifications are ambiguous (Uchida 1981). Gill raker counts can be used for identification of juveniles >25 mmSL, but gill rakers are too tiny and difficult to count in smaller specimens (Uchida 1981).

[3]Late larvae are defined as the "postflexion larvae" and "transformation larvae," and early juveniles as the "pelagic or special juveniles" of Kendall et al. (1984).

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

from Achotines Bay was pumped through a sand filter containing #20 silica sand and added to the tanks at a rate sufficient to exchange the water several times per day. Wild zooplankton, predominantly copepods, caught with a 505-μm mesh net were provided as food in densities of approximately 50–150/L two or three times per day until the black skipjack grew to about 13–17 mmSL. Then, whole *Poecilia latipinna* and *Poeciliopsis turrubarensis* fry or chopped fish of several species were provided four to six times per day. The black skipjack were fed until satiated. Maximum rations were provided throughout the growth experiments. When the fish reached about 35–45 mmSL, they were transferred into 3.0-, 4.6-, or 6.4-m diameter plastic-lined pools containing 2.3, 11.4, or 24.6 m^3 of water.

Water temperature in the laboratory aquaria was recorded to the nearest 0.1°C several times per day with a mercury thermometer. Salinity was measured to the nearest 1‰ (readability) several times per month with an optical salinometer. Daylight illumination was supplemented by fluorescent lights over the containers. At night, low levels of indirect fluorescent lighting were maintained to prevent the fish from colliding with the container walls.

Because black skipjack are delicate, initial lengths of those held for growth experiments were estimated by visually comparing them with a ruler held near the tank and adjusting for the magnifying effect of the water. Lengths of fish that had recently died or were near death in the tanks soon after capture were estimated in the same way, and subsequently measured (SL to nearest mm) after retrieval from the tanks to improve estimating skills and to provide a measure of estimation error. The maximum error measured was used to calculate the largest potential errors in growth rates that could have resulted.

Weights were calculated from lengths based on a weight-length relationship derived from 184 black skipjack measured (SL to nearest 0.1 mm) and weighed (round wet weight to nearest 0.001 g) soon after capture. Length and weight measurements were converted to natural logarithms (ln), and regression parameters ln$a$ and b were estimated by the method of least squares,

$$\ln W = \ln a + b \ln SL, \quad (1)$$

where W = weight in g, and SL = standard length in mm. Validity of the assumptions of linear regression were tested using residual analyses (Draper and Smith 1981).

Standard lengths and weights at the end of the growth experiments were measured to the nearest 0.1 mm and 0.1 g, respectively. The experiments were terminated when the fish died from some accidental or unknown cause or were near death.

The average daily growth rate of each fish over the duration of captivity was expressed as growth in SL (mm) during captivity divided by days in captivity. The average daily weight increase of each fish was calculated using final weights of the fish and the estimated SL at capture converted to weight.

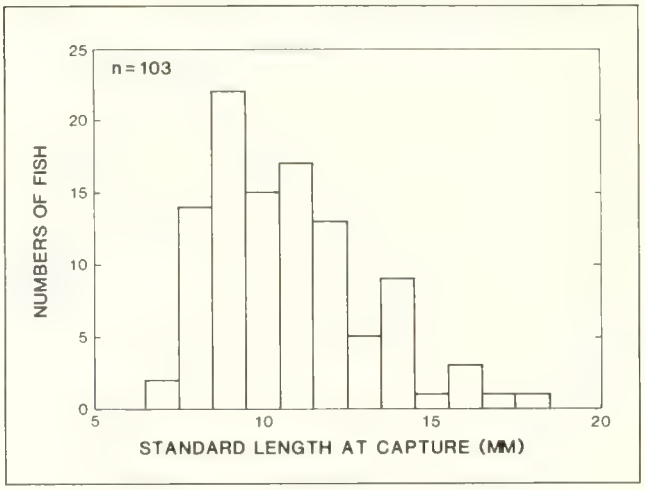

Figure 3
Standard lengths of late-larval and early-juvenile black skipjack tuna measured soon after capture by nightlighting in the waters south of the Achotines Laboratory, October 1987–April 1988.

Results

Late-larval and early-juvenile scombrids have been captured in all months of the year, but not in every month since the inception of routine sampling in 1984. During the period of October 1986–April 1988, 212 late-larval or early-juvenile black skipjack tuna were captured and transferred to the laboratory. Specimens which did not survive live transfer procedures ranged between 7.1 and 18.4 mmSL soon after capture (Fig. 3). A total of 79 (37%) survived handling and lived longer than 48 hours. Sampling dates, numbers caught, and other information are given in Table 1. Young black skipjack were caught during 16 of the 18 months in which sampling took place during this period. No nightlighting took place during January 1987 due to poor weather conditions. The greatest catches were made during November and December 1986, December 1987, and January 1988. Sampling frequency was governed by weather conditions, boat availability, and other factors. At times, sampling was terminated prematurely due to poor weather, which resulted in no catch. For this and other reasons, the

Table 1

Sampling information, numbers of late-larval and/or early-juvenile black skipjack which survived at least 48 hours after transfer to laboratory aquaria, and standard lengths of those which did not survive nightlighting and transfer procedures. Accurate measurements were not obtained from all those which did not survive.

Date	Sea-surface temp. (°C)	No. caught	Standard length at capture: Mean	Range	SD	*n*	No. surviving
1986							
8 Oct.	28.5	7	15.8	13.6–17.0	1.279	5	2
9 Oct.	28.3	0	–	–	–	–	–
11 Oct.	28.0	0	–	–	–	–	–
28 Oct.	28.4	17	11.4	9.4–15.3	1.631	16	1
29 Oct.	28.4	10	11.8	10.2–12.8	1.124	5	5
31 Oct.	28.4	0	–	–	–	–	–
5 Nov.	28.4	0	–	–	–	–	–
8 Nov.	28.4	0	–	–	–	–	–
19 Nov.	28.0	11	9.3	7.7–11.1	1.047	8	2
20 Nov.	28.0	2	–	–	–	–	1
26 Nov.	28.2	9	–	–	–	–	4
27 Nov.	28.4	4	–	–	–	–	0
4 Dec.	28.1	3	11.5	9.4–13.2	1.930	3	0
18 Dec.	27.6	2	10.5	10.0–11.0	0.707	2	0
22 Dec.	27.5	1	–	–	–	–	0
29 Dec.	27.5	0	–	–	–	–	–
1987							
6 Feb.	25.5	0	–	–	–	–	–
16 Feb.	25.5	0	–	–	–	–	–
17 Feb.	25.3	4	9.8	7.7–11.9	2.970	2	2
18 Feb.	–	0	–	–	–	–	–
9 Mar.	27.4	0	–	–	–	–	–
12 Mar.	24.5	0	–	–	–	–	–
25 Mar.	27.5	2	11.9	–	–	1	1
26 Mar.	27.1	0	–	–	–	–	–
30 Mar.	26.2	0	–	–	–	–	–
3 Apr.	–	0	–	–	–	–	–
8 Apr.	27.0	0	–	–	–	–	–
9 Apr.	26.4	0	–	–	–	–	–
1 May	28.4	0	–	–	–	–	–
4 May	29.0	2	9.4	–	–	1	1
6 May	29.0	0	–	–	–	–	–
1 June	28.9	0	–	–	–	–	–
3 June	28.5	0	–	–	–	–	–
4 June	28.5	0	–	–	–	–	–
25 June	29.7	0	–	–	–	–	–
26 June	29.3	0	–	–	–	–	–
2 July	29.5	0	–	–	–	–	–
7 July	29.0	3	12.0	–	–	1	2
9 July	28.8	0	–	–	–	–	–
1987 (continued)							
14 July	28.7	3	–	–	–	–	2
23 July	28.4	5	12.8	11.5–14.0	1.770	2	0
10 Aug.	28.6	0	–	–	–	–	–
11 Aug.	28.9	0	–	–	–	–	–
18 Aug.	28.4	0	–	–	–	–	–
20 Aug.	28.8	4	–	–	–	–	4
27 Aug.	28.6	0	–	–	–	–	–
31 Aug.	28.5	0	–	–	–	–	–
15 Sep.	28.5	3	10.5	–	–	1	2
17 Sep.	28.8	3	16.4	14.4–18.4	2.830	2	1
23 Sep.	29.0	6	8.1	–	–	1	1
2 Oct.	28.4	7	12.7	11.2–13.7	1.162	4	3
15 Oct.	28.9	0	–	–	–	–	–
23 Oct.	28.7	1	–	–	–	–	1
26 Oct.	28.5	1	–	–	–	–	0
9 Nov.	28.6	4	11.5	10.0–13.7	1.565	4	0
16 Nov.	28.2	3	–	–	–	–	3
17 Nov.	28.5	1	–	–	–	–	1
23 Nov.	28.0	0	–	–	–	–	–
9 Dec.	28.4	37	8.6	7.1–9.5	0.728	24	5
15 Dec.	28.5	8	10.3	9.5–11.7	1.217	3	5
16 Dec.	28.6	4	–	–	–	–	4
22 Dec.	28.5	4	8.0	7.9–8.0	0.071	2	2
1988							
1 Jan.	28.0	0	–	–	–	–	–
13 Jan.	27.6	0	–	–	–	–	–
18 Jan.	27.0	0	–	–	–	–	–
20 Jan.	27.3	36	11.3	9.0–14.4	1.717	13	23
25 Jan.	27.3	0	–	–	–	–	–
10 Feb.	26.0	1	12.2	–	–	1	0
8 Mar.	23.4	0	–	–	–	–	–
10 Mar.	24.4	2	10.9	–	–	1	1
16 Mar.	23.9	0	–	–	–	–	–
30 Mar.	23.5	0	–	–	–	–	–
5 Apr.	25.5	0	–	–	–	–	–
11 Apr.	27.1	1	9.2	–	–	1	0
13 Apr.	26.4	1	–	–	–	–	0
26 Apr.	26.6	0	–	–	–	–	–
28 Apr.	27.3	0	–	–	–	–	–
Total		212				103	79

capture frequency of black skipjack in Table 1 is not meant to reflect the true spawning frequency of the adults.

Thirty-nine specimens were held for laboratory growth experiments. Their estimated lengths and weights at capture are shown in Figure 4. The larger fish in the catch (Fig. 3) survived capture and transfer in greater proportions than the smaller ones (Fig. 4). The captive fish survived an average of 36 days in the laboratory; most (64%) died in 30 days or less. Three fish survived in excess of 130 days. The longest-lived black skipjack grew in captivity for 167 days, and attained an SL of 259 mm and weight of 336 g. It was sacrificed when it ceased feeding due to eye infec-

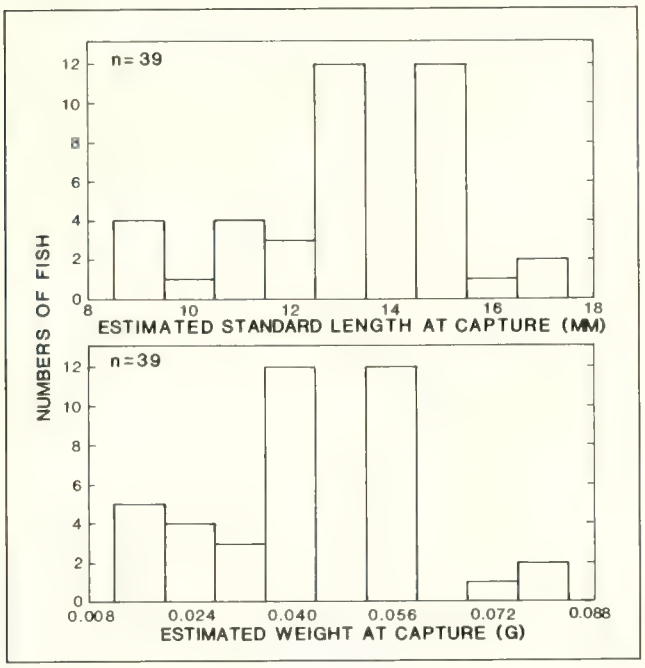

Figure 4

Standard lengths estimated in the laboratory and weights calculated from a weight-length regression (Fig. 6) for 39 black skipjack tuna held for growth experiments.

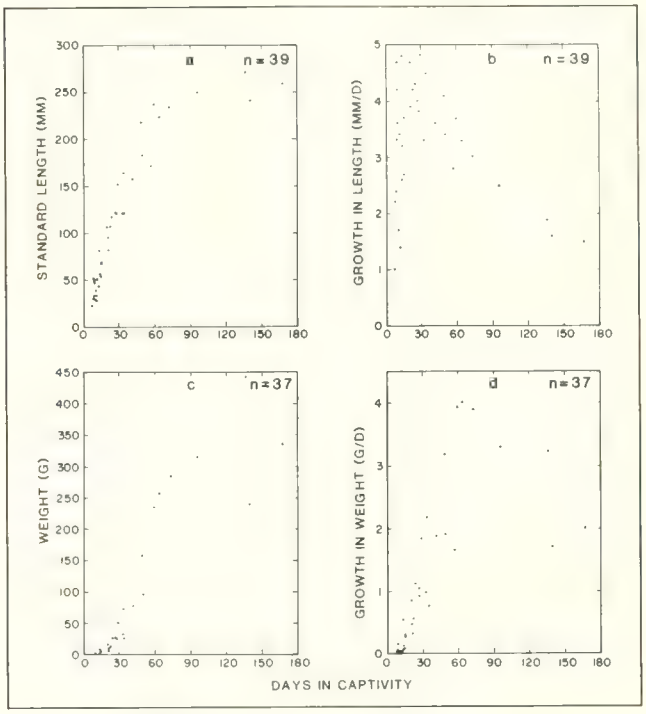

Figure 5

Standard lengths (a), growth rates in standard length averaged over the duration of captivity (b), weights (c), and growth rates in weight averaged over the duration of captivity (d) of juvenile black skipjack tuna at the end of laboratory growth experiments versus days in captivity. Two fish held 11 days were not weighed.

tions. Water temperature and salinity in the laboratory aquaria ranged from 23.7 to 29.1°C and 29 to 34‰, respectively, over all the experiments.

Growth in length

Captive black skipjack fed *ad libitum* grew in a curvilinear relationship of SL with time (Fig. 5a). The data were not fitted to derive a predictive growth equation because they are inadequate for that purpose. The fish were fed to satiation, but the rations were not measured.

The highest rates of growth in length were attained during the first month in captivity (Fig. 5b). After about 4 weeks, the fish had progressively lower average growth rates. Black skipjack from experiments that terminated during the first 15 days of captivity grew at extremely variable rates, from 1.0 to 4.8 mm/day. After 15 days, there was a significant negative correlation between growth rate and days in captivity ($r = -0.877$, $n = 23$, $P \ll 0.001$). All the fish that survived between 15 and 50 days grew rapidly, 3.2–4.8 mm/day. After about 50 days in captivity average growth rates declined drastically.

Errors in estimating lengths of newly-captured fish that had recently died or were near death in the tanks soon after capture ranged up to ±4 mm, although most were less. Maximum potential errors in growth rates were calculated based on the assumption that ±4-mm errors were made when estimating capture lengths of all the experimental fish. In general, the importance of measurement error diminished with increasing time in captivity. Potential errors ranged from only ±0.8 to a high of ±53.3% for one fish held the least time of all experimental fish (7.5 days). The next greatest error estimates were −26.1 and +23.8%, and the means were ±8.8%. Potential errors for the majority (85%) of the samples were ±13.5% or less, and less than 10% for all fish held in captivity more than 15 days ($n = 25$).

Growth in weight

Growth in weight appeared to follow a sigmoidal relationship with time in captivity (Fig. 5c). The rate of weight gain during the first 30 days was low, increasing dramatically between about 30 and 70 days, and then tapering off after 70 days.

While the greatest and most variable growth rates in length took place during the first 30 days, average rates of weight gain during that period were less than

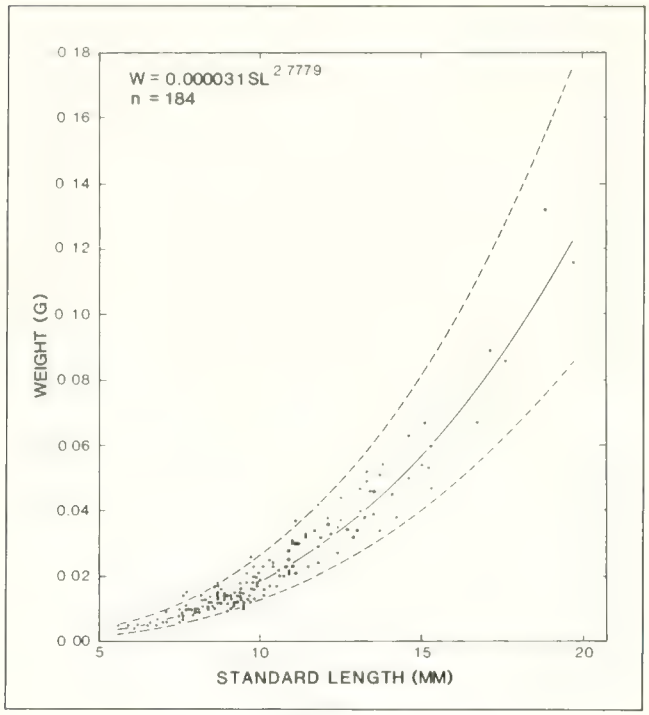

Figure 6

Weights (W) and standard lengths (SL) of 184 late-larval and early-juvenile black skipjack tuna measured soon after capture. The power function of the log-log fitted regression line and 95% prediction belts of weight on length are included. The r^2 of the log-log fit was 0.927, the 95% confidence limits of the regression coefficient were 2.6641–2.8917 g/mm, and the standard error of the estimate was 0.1790.

those for fish held longer (Fig. 5d). The greatest average growth rates in weight (3.9–4.0 g/day) were recorded for fish surviving 60–73 days ($n = 3$). After that time, average daily weight increases declined drastically ($n = 4$).

Weight-length relationship

Capture weights of the live black skipjack held for growth experiments (Fig. 4) were estimated using a weight-length regression equation based on fresh measurements and weights of 184 other black skipjack ranging from 5.6 to 19.7 mmSL and 0.004 to 0.132 g (Fig. 6). The power function of the fitted regression is $\ln W = -10.3806 + 2.7779 \ln SL$. The standard errors of parameters $\ln a$ and b are 0.1326 and 0.0577, respectively.

Tests for normality of the residuals (Filliben 1975), independence or lack of autocorrelation of the residuals (Durbin-Watson statistic), and a constant variance (homoscedasticity) of the residuals (Wesolowski 1976) failed to indicate any violation of the assumptions of linear regression.

Effect of temperature

Sea-surface temperatures during each sampling trip are shown in Figure 2. The data show a gradual decline in temperatures commencing in November or December, reaching lows of about 23–25°C in March, followed by a gradual warming to maximum stable temperatures of about 28–29°C from April or May until October or November. Black skipjack spanning the entire size range encountered (7.1–18.4 mmSL) were taken when the temperature ranged between 28.0 and 29.0°C. Only smaller individuals (7.7–12.2 mmSL) were caught when sea-surface temperatures were below 27.0°C, but the sample size was low ($n = 4$).

Neither the growth rates nor final sizes attained in captivity were significantly correlated with mean water temperatures in the aquaria over the course of the experiments. However, the final lengths ($r = -0.559$, $P<0.001$) and weights attained ($r = -0.572$, $P<0.001$), average daily growth in weight ($r = -0.503$, $0.001< P<0.002$), and the number of days in captivity ($r = -0.568$, $P<0.001$) were negatively correlated with minimum temperatures recorded in the laboratory. No such relationships were observed with the maximum temperatures recorded.

Discussion

Except for the black skipjack held in shipboard aquaria by Clemens (1956), these experiments are the first in which late-larval or early-juvenile tunas were collected in the wild and reared in captivity for experimental growth studies. Similar experiments on other scombrids are being conducted at the Achotines Laboratory. To our knowledge, 167 days is the longest time any scombrid has been held in captivity beginning at an early life stage. Harada et al. (1973) held *Auxis tapeinosoma* (= *A. rochei*) larvae for 52 days, Harada et al. (1974) reared *Sarda orientalis* larvae up to 99 days, and Harada et al. (1980) grew *Thunnus albacares* larvae for a maximum of 38 days. These larvae were all hatched from artificially-fertilized eggs obtained from ripe females, and fed unspecified rations of zooplankton and fish larvae. Previous to our studies, young *E. lineatus* were reared on only one occasion. Clemens (1956) collected black skipjack by dipnet at night, and held 10 individuals averaging about 27 mmSL for up to 12 days in shipboard aquaria. Average growth in length was 3.1–3.6 mm/day. The paper does not state at what water temperature the fish were held nor how much food was provided during the experiment. The growth rates measured in Harada et al.'s (1973, 1974, 1980) experiments were 3.0, 3.0, and 1.3 mm/days, respectively. The growth rates reported by Clemens

(1956) and Harada et al. (1973, 1974, 1980) are within the range of growth rates reported here, although we obtained greater rates too, up to 4.8 mm/day. Clemens (1956) stated that his results probably approximate minimum growth rates in nature.

An undesirable aspect of our study was the necessity of estimating, rather than measuring, lengths at the time of capture. This may have contributed to the large variance in the data reported for the first 15 days (Fig. 5b). Estimation errors were minimal, however, because the second author's ability to estimate lengths of live fish was continually refined by estimating, then measuring the fish that died in the tanks soon after capture. Except for a few fish held for short times, maximum estimation errors of ±4 mm translated to low potential error in growth rates.

Despite unavoidable estimation errors, this study reveals some interesting aspects of growth of young tunas. Black skipjack are capable of growing at high but variable rates when food is plentiful. The growth rates we measured might be considered upper limits for this species; feeding to satiation in the wild would likely be detrimental to survival because laboratory observations suggest that the added weight of food in the gut inhibits mobility. The variability in rates measured during the early part of the experiments may be due in part to the stress of captivity. However, high, variable growth rates suggest a large scope for growth (Brett 1979), an advantageous characteristic for fish that spend their early life stages in the epipelagic zone where predation risk is great. A large scope for growth permits rapid growth when food is abundant, providing young tunas an earlier transition to piscivorous feeding and early formation of schools. The decline in growth rates with increasing time in captivity may be related in part to inadequate-sized rearing containers (Theilacker 1980). Further laboratory growth experiments should concentrate on maintaining constant, controlled rations.

Growth rates of late juvenile and/or adult black skipjack from the commercial catch in the eastern Pacific Ocean are much lower, as expected, than those reported here. Tagging and length-frequency modal progression analyses provided rates that agree with each other (Peterson 1983:54–55). Black skipjack measuring 32–45 cmFL grew about 0.36 mm/day. Larger fish, 45–51 cm, grew more slowly, 0.22 mm/day. The upper seven data points in Figure 5a, corresponding to the largest fish (224–272 mmSL) which were held for the longest times (59.5–167.5 days), appear to represent a slower growth stanza than a previous stanza <60 days. A straight line fitted to these seven points yielded a significant slope of 0.28 mm/day, comparable to the natural growth rates reported for 32- to 51-cm black skipjack (Peterson 1983:54–55). Skipjack tuna *Katsuwonus pelamis*, another primitive species of the tribe Thunnini, measuring 37.5–42.5 cmFL when tagged and released east of 100°W longitude grew an average of 1.22 mm/day in 31–180 days at liberty (Bayliff 1988b).

Much additional work on growth of tunas under controlled conditions, as well as growth studies in nature, is needed to understand how physical and biotic variability in the ocean affects growth rates and life-stage duration. By virtue of black skipjack's biological similarities to commercially important tunas, we believe that such studies utilizing black skipjack tuna will yield important information that would be applicable to other tunas.

Acknowledgments

We wish to thank the staff members of the Achotines Laboratory for their hard work and long hours. R.R. Lauth and R.C. Jope provided special assistance with weight-length and laboratory temperature data. We acknowledge the efforts of G. Schumann, B.M. Chatwin, and J.M. Ianelli for much of the early development of the Achotines Laboratory. The Panamanian Ministerio de Comercio e Industria, Departamento de Recursos Marinos, has provided continued support of the Achotines Laboratory. Valuable reviews were provided by W.H. Bayliff, W.L. Klawe, R.R. Lauth, D. Margulies, K.M. Schaefer, and two anonymous reviewers.

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Length-weight, Age and Growth, and Landings Observations for Sheepshead *Archosargus probatocephalus* from North Carolina

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Sheepshead *Archosargus probatocephalus* range from Nova Scotia to Brazil (Robins and Ray 1986). Three subspecies have been recognized, based on the number and size of body bars: *A. p. probatocephalus* ranges along the Atlantic coast of the United States; *A. p. oviceps*, from St. Mark's, Florida to the Campeche Banks; and *A. p. aries*, from Belize to Babia de Sepetiba, Brazil (Caldwell 1958, 1965). Little is known concerning length-weight or age and growth relationships for this common edible fish.

This paper presents the age and growth and length-weight relationships, reviews changes in historical catch for sheepshead from North Carolina, and resolves discrepancies in the literature concerning maximum length and weight of this species (Hildebrand and Schroeder 1928, Hildebrand and Cable 1938, Bigelow and Schroeder 1953, Robins and Ray 1986).

Methods

Most specimens were captured in 12-m otter trawls, 91-m gillnets, or by spear. Most specimens were obtained from two sites where sheepshead are presently common in North Carolina: the Masonboro and Carolina Beach Inlets-Cape Fear River area of New Hanover and Brunswick counties, and Radio Island Jetty, Carteret County, extending from Beaufort Inlet in the Atlantic Ocean to just south of Shackleford Banks and Cape Lookout Jetty. The largest specimens and the state record-sized fish were caught in the Carolina Beach area by hook-and-line fishermen as part of the state's fishing citation program. Specimens were measured to the nearest millimeter standard (SL) and total length (TL) and weighed to the nearest gram, except for the tournament fish, which represented the upper end of the length-weight curve and were weighed to the nearest 114 g. Conversion from total length to standard length, for study fish larger than 100 mmSL, was possible by the formula $SL = 0.817TL$, $N = 240$; for fish smaller than 100 mmSL the conversion formula was $SL = 0.780$ TL. The latter conversion was determined by utilizing data for 412 young specimens (6–48 mm) measured by Hildebrand at Beaufort, North Carolina in 1914 (Hildebrand's field notes, Inst. Mar. Sci., Morehead City). Length-weight and standard length-scale radius relationships were calculated using log-log formulas where $\log(y) = a + b \log(x)$, where x is either standard length or scale radius, measured from the focus to the outer lateral edge of the scale, and y equals weight.

Scales were removed for ageing from just below the spinous/soft-ray dorsal-fin junction and the area above the lateral line. Scales were read at 10K magnification using a Baush and Lomb dissecting microscope. No validation of annulus formation was attempted considering the diverse availability of specimens. Therefore, the values I report are only presumed ages.

Results

The length-weight relationship for 282 sheepshead, measuring 9–591 mmSL (723 mmTL) and weighing 0.042–8370 g (18 lb, 7 oz), was calculated by the formula $\log(y) = -4.5287 + 3.0446 \log(x)$, $r = 0.9929$ (Fig. 1).

A linear relationship between standard length and scale radius was described for 68 fish measuring 31–525 mmSL by the formula $\log(y) = 0.8801 + 0.820 \log(x)$, $r = 0.9789$. Too few scales from specimens smaller than 30 mm were available for inclusion in the relationship calculation. Scales of fish 17–400 mmSL or those to age 4 were easy to read. Scales of older and larger specimens were difficult to read as the focus often became opaque and thickened, thereby obscuring the first two annuli.

Backcalculations of age and size from 50 of the best scales suggested seven age-classes (Table 1); however, these did not agree with a simple length-frequency plot where eight age classes seemed to prevail (Fig. 2). Also the maximum back-calculated size was 482 mm, whereas the largest fish studied was 525 mmSL. This discrepancy strengthened the observation that perhaps one or two annulae were obscured on scales of specimens larger than 400 mmSL, which were probably older than 8 years of age.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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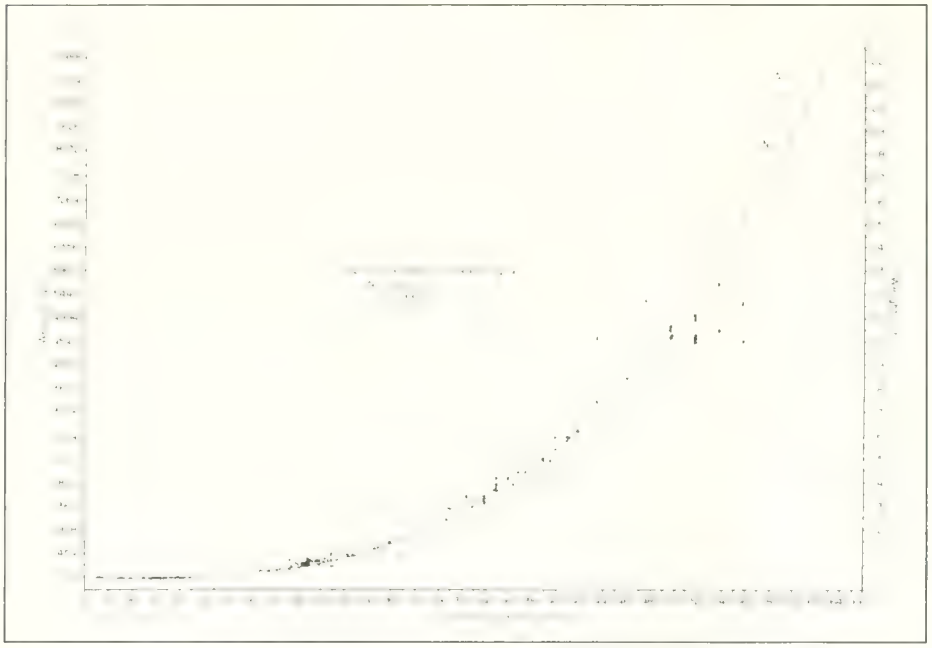

Figure 1
Length-weight relationship for 282 sheepshead captured in North Carolina. NC = largest North Carolina specimen; LA = world record Louisiana sheepshead.

Table 1
Backcalculation of standard lengths at presumed age for sheepshead from North Carolina.

		Age							
N	Y of Y	1	2	3	4	5	6	7	8
2	67	91							
30	73	156	189						
1	74	142	218	237					
1	106	158	205	248	295				
7	100	177	242	316	349	381			
7	81	135	242	274	325	366	387		
1	95	140	225	322	351	372	411	432	
1	97	138	222	266	355	397	422	466	482
		Weighted mean							
50	79	152	207	289	336	375	394	449	482
		Increment							
		73	55	82	47	39	19	55	33

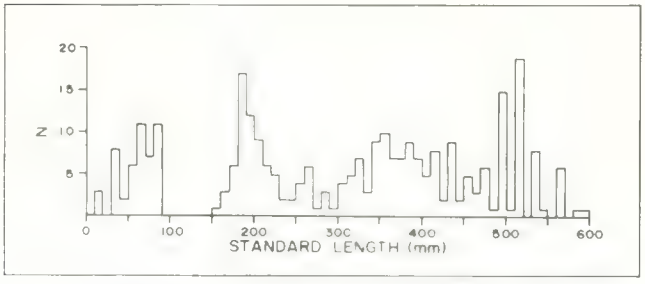

Figure 2
Length-frequency histogram in 10-mm intervals for 282 sheepshead captured in North Carolina.

Discussion

Only Ogburn (1984) has examined the length-weight of sheepshead from Masonboro Inlet Jetty, New Hanover County, NC. Her specimens measured 56–340 mmSL and weighed 4.3–1535 g, $N = 45$; data on five extremely small specimens, 56–63 mmSL, were excluded from the length-weight relationship. However, recalculation of this relationship, using all data, yielded the equation $\log (y) = -4.6927 + 3.1309 \log (x)$, $r = 0.9829$. Superimposing that recalculation on Figure 1 indicated good agreement between her data and that reported here.

Mook (1977) noted scales on 10–12 mm specimens. Johnson (1978) noted no scales for specimens of 12-mm lengths, but did depict them on a 17-mm specimen. North Carolina specimens smaller than 16 mm possessed no scales but their outlines were present on 11–12 mmSL specimens.

A variety of structures have been used to age fishes (Summerfelt and Hall 1987). The reason only scales were used to age sheepshead was that they were the only structures consistently available during this study, as the fish were obtained from many sources or could not be kept for age determination by vertebra, otoliths, etc.

The largest sheepshead from nearby South Carolina were 513 mmSL (641.4 mmTL) weighing 6015.5 g, and 505 mmSL (625 mmTL) weighing 4900 g (D. Hammond and E. Wenner, S.C. Wildl. Mar. Res. Dep., Charleston, pers. commun., Jan. 1990). These data also fall within the length-weight curve plotted for North Carolina sheepshead (Fig. 1).

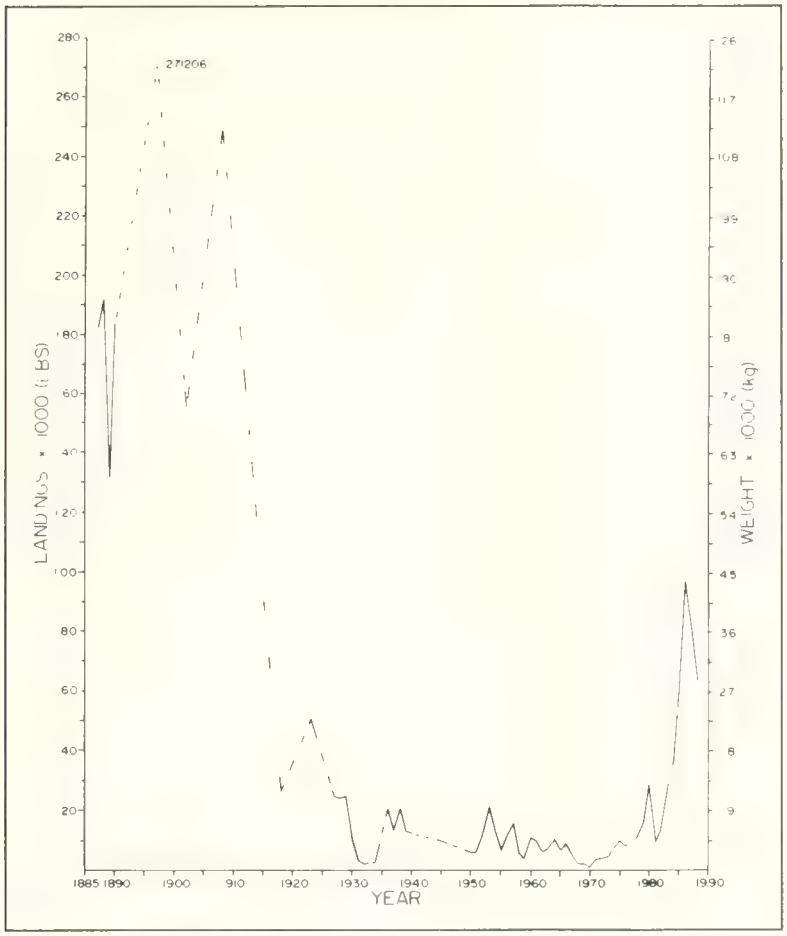

Figure 3
North Carolina catch landings for sheepshead, 1887–1989. Dashed lines indicate missing year data.

Like Hildebrand and Cable (1938) for Beaufort, NC, and Springer and Woodburn (1960) for Gulf of Mexico sheepshead, the smallest North Carolina sheepshead were also captured between May and October. Note the peculiar hiatus in the length frequency and length-weight curve (Figs. 1, 2) for sheepshead 90–150 mmSL. Absence of specimens within these size ranges may have been caused by their shifting from a seagrass habitat to piling, jetty, and other hard substrates preferred by larger young and adults (Hildebrand and Cable 1938, Johnson 1978).

A search of major museums and taxidermist records has failed to uncover sheepshead that attain the size and weight (91 cm and 9–13.5 kg) reported in the literature (Hildebrand and Schroeder 1928, Hildebrand and Cable 1938, Bigelow and Schroeder 1953, Robins and Ray 1986). Even if 91 cm was an accurate total-length measurement, conversion to SL would make that specimen 743 mm, a size far larger than even the officially recognized world-record specimen from Louisiana (probably *A. p. oviceps*), which was 596 mmSL and 730 mmTL, and weighed 9648 g (21 lb, 4 oz, and plotted in Figure 1) and would fall far outside the length-weight data depicted in Fig. 1. This is strong evidence that sheepshead do not attain the large sizes mentioned in the literature. In essence, future literature should be emended to note that the maximum sizes of sheepshead in North Carolina, to date, are 591 mmSL, 723 mmTL, weighing 8370 g, and elsewhere 596 mmSL, 730 mmTL, weighing 9248 g. All larger sizes reported should remain or be considered erroneous.

A dramatic shift in the commercial landings of sheepshead (mostly caught by haul seine) has occurred in North Carolina between 1887 and 1989 (Fig. 3) (Chestnut and Davis 1975; Goode 1884; NC Div. Mar. Fish. statistical data, Morehead City). Yarrow noted (Smith 1907) that sheepshead were very abundant in 1871. Commercial catches prior to 1900 remained over 61500 kg. Catches between 1918 and 1981 remained low (27000–47000 kg, lowest in 1970, 675 kg). Only since 1981 has a recent surge been noted in the landings (Fig. 3), mostly in Carteret County.

Hildebrand and Cable (1938) and Johnson (1978) noted that larval and juvenile sheepshead are usually found associated with seagrasses which they depend

upon for shelter and food. Whether the early and recent landings can be correlated with seagrass abundance remains unknown, for no early records of seagrass abundance exist prior to and following the wasting disease of the 1930s (Orth and Moore 1981, Short et al. 1987). To date, the beds have seemingly not increased (G. Thayer, NMFS Beaufort Lab., pers. commun., Jan. 1990). It would have been beneficial to know whether the early-life-history stages that depend on vegetation for food and protection were or are increasing in relation to seagrass incidence and just how dependent they are on that habitat for their growth and survival.

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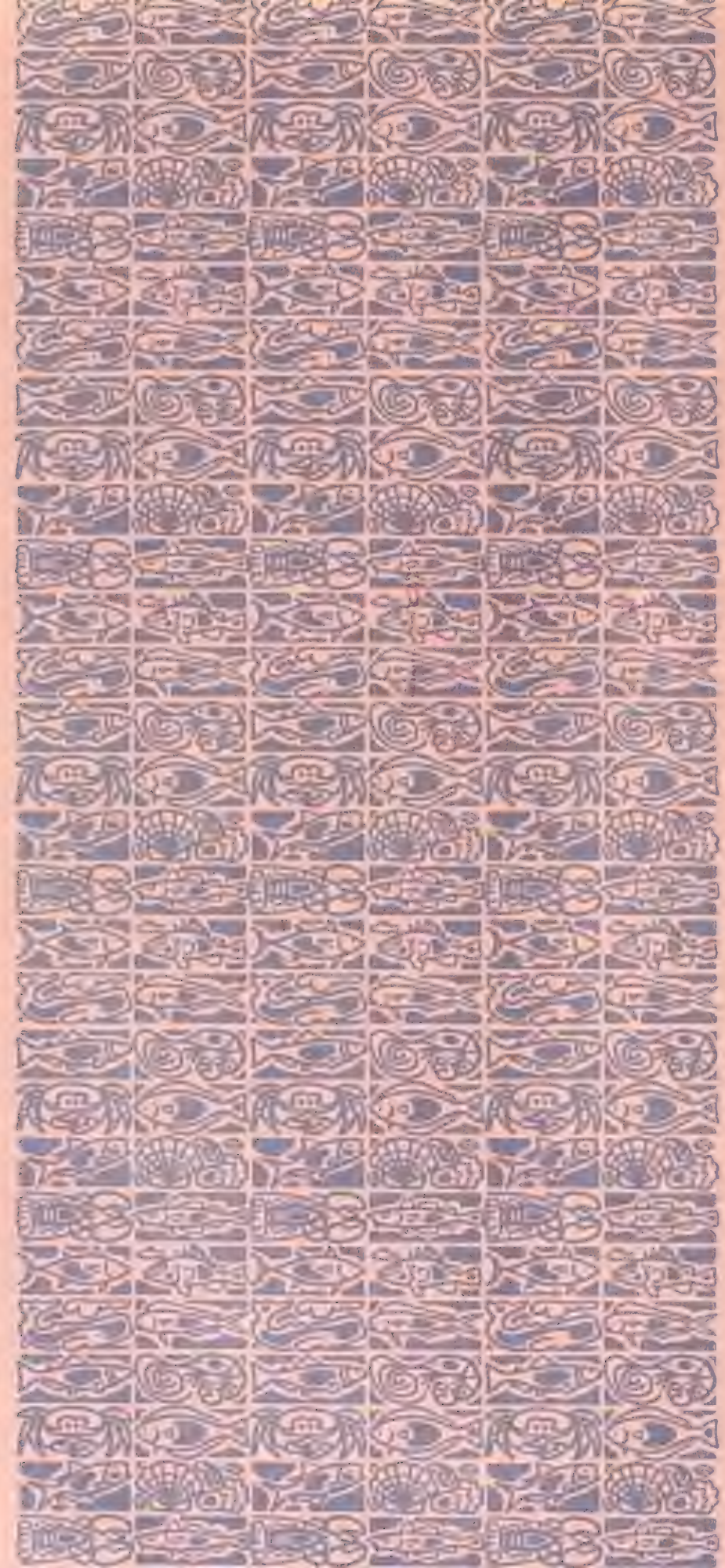

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